Cortical oscillatory changes associated with cognitive effort, value of effort, and incentive.

Thesis submitted in accordance with the requirements of the University of Liverpool for the degree of Doctor in Philosophy by Adam Byrne

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Declaration

This dissertation is the result of my own work and includes nothing which is the outcome of work done in collaboration except where specifically indicated in the text. No part was submitted in support of any other applications for degree or qualification at this or any other university or institute of learning.

In accordance with The University of Liverpool guidelines, this thesis does not exceed 100,000 words.

Signed: Adam Byrne

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List of Abbreviations

In alphabetical order:

ACC	**Anterior Cingulate Cortex**
ADHD	**Attention Deficit Hyperactivity Disorder**
ATP	**Adenosine Triphosphate**
AuC	**Area Under the Curve**
BOLD	**Blood Oxygen Dependent**
COGED	**Cognitive Effort Disconting**
Cm	**Centimetre**
CV	**Cardiovascular**
ECG	**Electrocardiogram**
EEG	**Electroencephalography**
EMG	**Electromyography**
EoG	**Electrooculogram**
ERD	**Event-Related Desynchronization**
ERP	**Event-Related Potential**
ERS	**Event-Related Synchronisation**
fMRI	**Functional Magnetic Resonance Imaging**
FPN	**Fronto-Parietal Network**
GABA	**Gamma-Aminobutyric Acid**
Hz	**Hertz**
IFC	**Inferior Frontal Cortex**
M1	**Primary Motor Area**
MCC	**Medial Cingulate Cortex**
MEG	**Magnetoencephalography**
MID	**Monetary Incentive Delay**
OFC	**Orbitofrontal Cortex**
PCC	**Posterior Cingulate Cortex**
PET	**Positron Emission Tomography**

PFC	**Prefrontal Cortex**
RT	**Reaction Time**
SMA	**Supplementary Motor Area**
STN	**Subthalamic Nucleus**
SV	**Subjective Value**
TMS	**Transcranial Magnetic Stimulation**
μV	**Micro-Volts**
VS	**Ventral Striatum**

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Abstract

Adam Byrne, Cortical oscillatory changes associated with cognitive effort, value of effort, and incentive.

Cognitive effort is conceptualised as being deployed relative to the SV of its associated outcomes. The SV of incentives should therefore directly modulate effortful performance, as well as cortical processes associated with effortful engagement. However, the relationship between incentive value and modality, and effortful engagement remains unclear. The current thesis aimed to elaborate on the deployment of cognitive effort in response to incentives of differing magnitude and valence using preparatory ERD/ERS measures in tandem with discounting procedures.

ERD/ERS in the alpha and beta bands was used to untangle cortical activation from inhibition during effortful engagement, as well as separating anticipatory attention from approach/avoidance motor responses under rewards of differing magnitudes and valence. Further, a COGED discounting task was used to estimate effort discounting rates, and to compare the SV of gains and losses.

The results presented in the three experimental chapters showed that rewards lead to different modulations in pre-movement ERD/ERS depending on the task-structure used. Losses were more motivating than gains, but were associated with slower RTs, as well as deteriorations in alpha-band ERD. Further, individual SVs of effort were not significantly associated with changes in RT or ERD under differing incentives.

The current thesis showed that cognitive effort is deployed through patterns of strategic cortical activation and inhibition, rather than a sustained increase in cortical activation. Further, the divergent effect of losses and gains was revealed to likely be due to attentional effects not the previously hypothesised approach/avoidance associations. Finally, the SV of effort does not appear to directly inform effortful engagement.

Chapter 1 – General Introduction

1.1 Cognitive Effort

1.1.1 The concept of effort

The concept of effort is an intuitive one, considered to be the amount of work, either physical or cognitive, an individual must expend to reach a desired goal. It has been known since the early-twentieth century that prolonged effort causes fatigue and deteriorations in performance (Arai, 1912). An aversion to effort was then found across several species, leading Hull (1943) to propose the 'law of less work', stating that organisms will always choose the option which requires the least effort to achieve, given that the subjective value of offered outcomes is equal.

The tendency to avoid effort is a general principal in human behaviour. For example, individuals will usually choose to reach in directions which involve moving the least mass (Wang & Johnson, 2012), will walk along paths which require making the fewest number of steps (Bitgood & Dukes, 2006), and will move an object over the shortest possible distance (Rosenbaum & Gaydos, 2008). Similarly, when offered tasks which require cognitive effort, individuals will show a preference for the option which requires the least effort (Botvinick, Niv, & Barto, 2009; Chong et al., 2017; Dixon & Christoff, 2012; Kaufman, 1999; Kool & Botvinick, 2014; Lane, 1992; Loewenstein, Rick, & Cohen, 2008; Massar, Libedinsky, Weiyan, Huettel, & Chee, 2015), even to the point of expending physical effort to reduce subsequent cognitive effort (Botvinick, 2007; Risko, Medimorec, Chisholm, & Kingstone, 2014).

However, it has been argued that effort is a rather abstract idea, which has been used to describe multiple distinct concepts that cannot necessarily be reconciled (Baumeister, Bratslavsky, Muraven, & Tice, 1998; Baumeister, Muraven, & Tice, 2000; Preston, Wegner, Morsella, Bargh, & Gollwitzer, 2009). First, there are stark

differences between cognitive and physical effort, such as the metabolic costs associated with physical effort that are not found during sustained cognitive effort (Boska, 1994; Jeneson, Westerhoff, Brown, Van Echteld, & Berger, 1995; Potma, Stienen, Barends, & Elzinga, 1994; Russ, Elliott, Vandenborne, Walter, & Binder-Macleod, 2002; Szentesi, Zaremba, van Mechelen, & Stienen, 2001). Second, while cognitive effort is usually considered to be the subjective feeling of effort associated with the engagement of cognitive resources, it has also been associated with the amount of cognitive resources dedicated to a task (Arai, 1912; Blain, Hollard, & Pessiglione, 2016; Hagger, Wood, Stiff, & Chatzisarantis, 2010; Scerbo, 2001), measures of effortful performance (e.g., RTs, items remembered from a list, mathematical speed ect.) (Bandura, 1977; Bijleveld, Custers, & Aarts, 2010; Eisenberger, 1992; Kukla, 1972; Locke & Latham, 1990), and the discounting effect of effort requirements associated with a reward (Prévost, Pessiglione, Météreau, Cléry-Melin, & Dreher, 2010; Walton, Kennerley, Bannerman, Phillips, & Rushworth, 2006).

It should also be noted that there are situations where effort expenditure may increase the value of an associated reward (Arkes et al., 1994; Kameda, Takezawa, Tindale, & Smith, 2002; Mochon, Norton, & Ariely, 2012; Muehlbacher & Kirchler, 2009; Norton, Mochon, & Ariely, 2012). Further, in contrast to physical effort, the exact cost of cognitive effort remains unclear, although multiple theories have been proposed to explain its aversive nature (Christie & Schrater, 2015; Gailliot & Baumeister, 2007; Kurzban, 2016).

In the present thesis effort is considered to be the amount of physical or cognitive resources dedicated to a task in the pursuit of a specific outcome, and the subjective feeling of effort (phenomenological effort) associated with it. Effort was

not directly investigated during the research discussed, which focused on effort-discounting rates, effortful performance, and ERD measures associated with incentives. While providing useful insight into the phenomena, these measures cannot be used to make categorical claims about the amount of effort dedicated to a task. The research discussed in the present thesis instead aimed to elaborate on the cortical effects underpinning effortful performance under incentives of differing magnitudes and valences, and how this is associated with individual effort discounting rates.

1.1.2 Cognitive effort

Cognitive effort is familiar to most people, experienced when performing a series of calculations, reading a difficult book, or writing an essay. The prolonged implementation of cognitive effort usually leads to significant fatigue and aversion to further effortful engagement (Arai, 1912; Blain, Hollard, & Pessiglione, 2016; Hagger, Wood, Stiff, & Chatzisarantis, 2010; Scerbo, 2001). The fatigue associated with effortful engagement is usually described as a subjective feeling, with associated wincreased aversion to cognitive effort (Smit, Eling, & Coenen, 2004). Cognitive fatigue is related to both the workload and duration of an effortful task (Earle, 2004), as well as the amount of control individuals have over the task (Karasek, 1979; Theorell & Karasek, 1996). However, despite the phenomenological fatigue associated with cognitive effort, the brain can perform numerous complex calculations simultaneously without an experience of phenomenological effort. For example, the visual system performs a multitude of complex calculations with no experienced effort, whilst scanning a visual field often results in extreme feelings of effort and fatigue (Ackerman, 2011).

Cognitive fatigue is often viewed as the depletion of a resource or energy store associated with cognitive effort (e.g., glucose-depletion, or amyloid-beta protein build-

up) (Gailliot & Baumeister, 2007) but is also highly modulated by motivational and task-perception factors. For example, when cognitive activities are self-initiated, consistent with internal goals or regarded as 'play' they often do not lead to significant levels of reported fatigue (Frankenhauser, 1986). Cognitive fatigue may therefore not be directly related to the depletion of a specific limited resource, or certain motivational and task-perception factors may counteract the phenomenological fatigue associated with cognitive effort even though the resource associated with it remains partially depleted. The exact nature of cognitive fatigue is not well understood, and the concept lacks a strong operational definition beyond a subjective experience and its related aversion (Hockey, 2011).

Theories of cognitive effort also disagree on the relation between cognitive fatigue and physiological processes. Resource-limited models posit that cognitive fatigue is a fundamental result of the depletion of a limited resource, be it the loss of cortical glucose stores or the build-up of amyloid beta proteins reducing the brain's ability to engage in effortful tasks (Gailliot & Baumeister, 2007). However, opportunity cost models of cognitive effort view cognitive fatigue as being a purely motivational process, or as an experience produced by the brain to discourage the future deployment of cognitive effort.

For this reason, it has been argued that the key component behind whether a task is perceived as effortful is whether it requirges the implementation of cognitive control (Hasher, 1979; Kaplan & Berman, 2010; Schneider & Shiffrin, 1977). This appears to be the primary mediator in participants' decisions to engage or disengage in effortful tasks (Dixon & Christoff, 2012; Inzlicht, Schmeichel, & Macrae, 2014; Kool, McGuire, Rosen, & Botvinick, 2010; Shenhav, Botvinick, & Cohen, 2013b; Westbrook et al., 2013).

Cognitive control can be conceptualised as the degree of top-down control over neural or cognitive resources (Bogacz, Brown, Moehlis, Holmes, & Cohen, 2006; O'Reilly & Frank, 2006), and is commonly viewed as being a conscious rather than an automatic process (Botvinick & Cohen, 2014; Cohen, Dunbar, & McClelland, 1990; Norman & Shallice, 1986; Posner, Snyder, & Solso, 2004). Cognitive control is a distinct concept from cognitive effort, although it is commonly conceived as the underlying cognitive resource associated with cognitive effort. Cognitive control and effort are fundamentally linked and increased cognitive control may result in associated feelings of phenomenological effort and fatigue. However, other factors may also be associated with the amount of phenomenological effort an individual experiences during a task, such as mood or framing effects (Akerlof & Yellen, 1990; Blau, 1993; Byrne, Stoner, Thompson, & Hochwarter, 2005; Hannan et al., 2005; Lindquist, 2010). Cognitive control should therefore not be considered as directly related to phenomenological effort, but rather as the underlying cognitive resource mediated by subjective experiences of effort and fatigue.

Previous research has established a link between cognitive control and effort by demonstrating an increase in pupil dilation (Brown et al., 1999; Laeng, Ørbo, Holmlund, & Miozzo, 2011; Rondeel, van Steenbergen, Holland, & van Knippenberg, 2015; Siegle, Ichikawa, & Steinhauer, 2008; Siegle, Steinhauer, & Thase, 2004; van Bochove, Van der Haegen, Notebaert, & Verguts, 2013; van Steenbergen & Band, 2013; van Steenbergen, Band, & Hommel, 2015; Wendt, Kiesel, Geringswald, Purmann, & Fischer, 2014) and changes in CV activity reflecting depressions in sympathetic activity (Kuipers et al., 2017) in response to conflicting trials in cognitive control paradigms.

The PFC is important in the implementation of cognitive control (Miller & Cohen, 2001), leading some to argue that cognitive control is the cardinal function of this region (Cohen & Servan-Schreiber, 1992; Grafman, 1994; Miller, 1999; Passingham, 1993; Wise, Murray, & Gerfen, 1996). Similarly, the ACC has been described as being largely responsible for conscious behaviour (Botvinick & Braver, 2015; Dehaene et al., 2003; Frith, 2002; Holroyd & Braver, 2016; Holroyd & Yeung, 2012; Shenhav, Botvinick, & Cohen, 2013a; Shenhav et al., 2017; Vassena, Holroyd, & Alexander, 2017; Verguts, Vassena, & Silvetti, 2015), as well as the optimisation of cognitive effort (Botvinick, Braver, Barch, Carter, & Cohen, 2001; Gehring & Willoughby, 2002; Holroyd & Coles, 2002; Mega & Cummings, 1997). The ACC is therefore proposed to implement the monitoring component of cognitive control (Botvinick, 2007; Botvinick et al., 2001; Botvinick, Cohen, & Carter, 2004). A key step of cognitive control arises from the communication between the dorsolateral ACC and the lateral PFC, where the dorsolateral ACC is described as monitoring the need for control, while the lateral PFC implements it (Botvinick et al., 2001; Kerns et al., 2004).

Research suggests that performing tasks in a context with incentives present leads to enhancements in specific cognitive processes such as active maintenance in working memory, preparatory attention, episodic encoding, and decision-making (Locke & Braver, 2010; Maddox, Baldwin, & Markman, 2006; Pessoa, 2009; Pessoa & Engelmann, 2010; Shohamy & Adcock, 2010). For example, the effects of monetary incentives on listening effort has been tested, showing that high monetary incentives can be used to boost task performance, as well as CV responses associated with effortful engagement (Pichora-Fuller et al., 2016; Richter, 2016). The effect of incentives on cognitive effort appears to occur via modulations of specific neural

circuits involving the PFC, midbrain dopamine system, and related subcortical structures such as the basal ganglia and hippocampus, causing an interaction between cognitive control and reward (Berridge, 2007; Boehler, Schevernels, Hopf, Stoppel, & Krebs, 2014; Daw, O'Doherty, Dayan, Seymour, & Dolan, 2006; Dreisbach & Fischer, 2012; Engelmann et al., 2009; Guitart-Masip, Chowdhury, et al., 2012; Krawczyk, Gazzaley, & D'Esposito, 2007; dpher et al., 2003; Niv, Daw, Joel, & Dayan, 2007; Padmala & Pessoa, 2010).

However, while the neural underpinnings and costly nature of cognitive effort and control are clear (Dixon & Christoff, 2012; Inzlicht et al., 2014; Kaplan & Berman, 2010; Kool et al., 2010; Shenhav et al., 2013b), it is unclear why cognitive control itself is effortful or aversive. Several theories have been proposed to explain the aversive and fatiguing nature of cognitive effort (Christie & Schrater, 2015; Gailliot & Baumeister, 2007; Kurzban, 2016), however each has its own limitations and no single theory comprehensively explains the aversive nature of cognitive effort.

While cognitive effort is usually seen as a resource that is deployed in response to associated incentives, leading to improvements in effortful performance, the cortical underpinnings behind the effect of incentives on effortful performance is not well-understood. The research discussed in the present thesis investigated this relationship using ERD measures of cortical activation/inhibition during periods of sustained engagement with an effortful task under differing levels of reward.

1.1.3 Physical effort

There are many situations where one must exert effort, be it cognitive or physical, to receive a desirable outcome. For example, an athlete may train harder to win a marathon if they are incentivised with a monetary prize, or a student may revise harder for an exam when an important incentive is offered (Berridge, 2004; Schmidt,

Lebreton, Cléry-Melin, Daunizeau, & Pessiglione, 2012; Tran, Hagen, Hollenstein, & Bowie, 2020; Botvinick, Niv, & Barto, 2009; Lewis, 1964; Jansma, Ramsey, de Zwart, van Gelderen, & Duyn, 2007). However, it is currently unclear whether these two kinds of effort are driven by common or distinct neural regions.

Physical effort is often considered to be similar to cognitive effort because it is similarly aversive and discounting of associated rewards (Hartmann, Hager, Tobler, & Kaiser, 2013; Morel, Ulbrich, & Gail, 2017) and because participants who show a stronger aversion to cognitive effort also show a stronger aversion to physical effort (Nishiyama, 2016). While there is neural overlap between the two kinds of effort, this overlap also occurs with other forms of discounting (e.g., delay, probability) (Miller, Thome, & Cowen, 2013), and the neural circuitry underlying cognitive and physical effort appears distinct (Hosking, Cocker, & Winstanley, 2014; Schmidt, Lebreton, Clery-Melin, Daunizeau, & Pessiglione, 2012). The distinct neural patterns involved in cognitive and physical effort mean that these areas may simply be responsible for the encoding and valuation of rewards, or in weighing immediate against long-term outcomes.

Although there is an association between cognitive and physical effort, there are fundamental differences between the two which cannot necessarily be reconciled. For example, the costs of physical effort are much clearer than those associated with cognitive control. The energy that enables bodily functions and activities during physical effort stems from carbohydrates, fats & proteins, transferred via adenosine triphosphate and consumed proportional to force magnitude (Boska, 1994; Jeneson, Westerhoff, Brown, Van Echteld, & Berger, 1995; Potma, Stienen, Barends, & Elzinga, 1994; Russ, Elliott, Vandenborne, Walter, & Binder-Macleod, 2002; Szentesi, Zaremba, van Mechelen, & Stienen, 2001). The costly nature of cognitive

effort is much less clear, with some researchers arguing that its costs emerge from the depletion of limited cortical resource and others arguing that cognitive effort is only perceived as aversive due to the opportunity costs associated with it.

However, similar to the limitations associated with self-report measures of cognitive effort, the direct costs of physical effort may be ambiguous or difficult to examine in certain situations. For example, people tend to judge hills to be steeper when they are wearing a heavy backpack (Bhalla & Proffitt, 1999; Witt, 2017), and higher physical effort may affect judgements of cognitive effort, where holding a heavy object leads to a higher degree of cognitive elaboration (Jostmann, Lakens, & Schubert, 2009). Further, meta-analytic reviews on the role of physical workload in the perception of time support the view that physical effort has similar effects on task-perception as cognitive effort, as both demand attention and therefore constrain cognitive processing (Block, Hancock, & Zakay, 2016; Skulmowski & Rey, 2017), meaning the differential effects of cognitive and physical effort cannot easily be untangled.

Alongside the depletion of ATP stores, the self-perception of cardiovascular and respiratory activity seems to play an important role in the sensation of physical effort (Kollenbaum, Dahme, & Kirchner, 1996; Kollenbaum, Dahme, Kirchner, Katenkamp, & Wagner, 1994; Pennebaker, 1981). For example, Pennebaker and Lightner (1980) demonstrated that, when jogging to a constant pace on a treadmill, individuals reported increased feelings of fatigue when listening to their own breath compared to other sounds. The results reported by Pennebaker and Lightner (1980) suggests that the self-perceptions of respiratory processes may confound the subjective experience of physical effort, similar to the effect of motivational factors on cognitive effort (Brooks, Stremitzer, & Tontrup, 2017; Church, Libby, & Zhang, 2008; Gose &

Sadrieh, 2012; Hannan, Hoffman, & Moser, 2005; Van de Weghe & Bruggeman, 2006).

The present thesis primarily examined cognitive rather than physical effort. However, tasks requiring speeded responses may also require some degree of physical effort, necessary to organise a fast motor response, in addition to the cognitive effort required to maintain attention and detect the target stimulus as quickly as possible. The relation between physical and cognitive effort should therefore be understood when using RT tasks to investigate effortful behaviour.

1.1.4 Theories of cognitive effort

There are two main schools of thought to explain why people generally find cognitive effort aversive (Westbrook & Braver, 2015). The first states that cognitive effort is aversive due to the depletion of a specific resource in the brain, for example blood-glucose supplies (resource-limited models). The second states that cognitive effort is perceived as aversive due to the opportunities lost from engaging limited cognitive resources (opportunity cost models).

1.1.4.1 Resource-limited models.

Resource-limited models posit that effortful tasks are perceived as aversive due to the depletion of a specific metabolic resource. In resource-limited accounts, cognitive effort becomes increasingly aversive as time goes on due to the depletion of limited metabolic resources, causing experiences of increased fatigue and aversion. Effortful outcomes are posited to be seen as aversive in choice tasks as they would lead to the necessary depletion of a metabolic resource, stores of which must then be replenished at a cost. Further, engaging in effortful tasks will lead to a reduced ability to deploy effortful resources in the future due to cognitive fatigue, meaning resource-

limited models also posit an opportunity cost of effort, leading to increased aversion over time.

Support for resource limited models comes from the finding that cognitive fatigue occurs following an effortful task, and remains even when participants are required to engage in a second, different effortful task (Gailliot & Baumeister, 2007). This suggests that the fatigue caused by sustained cognitive effort is not task-specific, and may instead be related to an underlying resource that is depleted over time.

A popular early account of effort was the idea of 'ego-depletion', or that the strength of self-control is depleted over time, leading to a reduced ability to engage in controlling behaviour, although the exact resource being depleted was never specified (Hagger et al., 2010).

The blood-glucose model was proposed to explain the resource being depleted when participants exert self-control (Gailliot & Baumeister, 2007). This posits that engaging in cognitive effort results in increased neural activation, leading to the depletion of blood-glucose. In support of this model, previous research has found a relationship between the implementation of cognitive effort and blood-glucose levels (Fairclough & Houston, 2004; Gailliot & Baumeister, 2007). Further, moderate hypoglycaemia, a fall in blood sugar levels below normal, is associated with reduced preferences for engaging in effortful tasks (Brain, 1999).

However, contrary to the hypotheses of the blood-glucose model of cognitive effort, only slight changes to global metabolic demands of the brain have been found during cognitively demanding tasks (Gibson, 2007; Kurzban, 2010; Rachlin, 2006). In contrast, several other biological and physiological markers, such as CV activity, have been shown to be modulated by cognitively demanding tasks (Capa, Audiffren, & Ragot, 2008; Critchley et al., 2003; Fairclough & Roberts, 2011; Gendolla, Wright, &

Richter, 2012; Iani, Gopher, & Lavie, 2004; Wright, 1996), meaning that changes in blood glucose associated with effort may be due to arousal or stress (Gibson, 2007).

To overcome these problems, it has been argued that engaging in cognitive effort may result in the depletion of local glycogen stores, rather than the brain's global glucose intake (Christie & Schrater, 2015; Gibson, 2007; Raichle & Mintun, 2006). However, while there is some evidence to support the idea that cognitive effort results in the depletion of glycogen stores (Roach, 2002), these only account for 1-6% of energy usage in the brain. Local changes in cerebral metabolism due to cognitive control are also small (Raichle & Mintun, 2006), meaning glycogen stores are usually capable of dealing with the depletion caused by prolonged cognitive effort (Benington & Heller, 1995). There is, therefore, little reason to think that the depletion of these stores would lead to significant aversion or fatigue.

An alternative resource-limited model of cognitive effort posits that cognitive effort is aversive as it causes a build-up of amyloid-beta proteins in the brain (Holroyd & Umemoto, 2016). A long-term build-up of amyloid-beta proteins has been associated with neuronal damage and cognitive decline (Bu et al., 2015; Cheignon et al., 2018; Shoji et al., 1992; Spires-Jones & Hyman, 2014), as well as the development of Alzheimer's disease (Cheignon et al., 2018; Mori, Takio, Ogawara, & Selkoe, 1992; Spires-Jones & Hyman, 2014). Amyloid-beta plaques usually build up during the day and are cleared during sleep (Cedernaes et al., 2017; Xie et al., 2013), and sleep-deprivation has been associated with increased phenomenological effort and aversion to effortful tasks (Libedinsky et al., 2013; Massar, Lim, & Huettel, 2019; Massar, Lim, Sasmita, & Chee, 2019). However, sleep deprivation is also associated with other symptoms such as stress and fatigue which may explain an increased aversion to effort (Franzen et al., 2011; McEwen & Karatsoreos, 2015; Samkoff & Jacques, 1991).

1.1.4.2 Opportunity cost models.

Opportunity cost models of cognitive effort are based on the idea that a task becomes perceived as effortful when the opportunity costs of engaging cognitive resources outweighs their potential benefits (Lazarus, 1993; Tooby & Cosmides, 2008). Opportunity cost models posit that the subjective experience of effort and fatigue are produced by the brain as a 'stop-function' to motivate the organism to avoid the cognitively demanding task (Inzlicht et al., 2014; Lazarus, 1993; Tooby & Cosmides, 2008), similar to the proposed functional role of boredom (Elpidorou, 2018).

The cost of effort proposed in these models is the loss of the opportunity to forage for new information or engage in another, more rewarding, task (Kurzban, 2016). This is because cognitive effort is generally associated with conscious processes which cannot be run in parallel, and, therefore, require prioritization (Evans, 2008; Miller, 1956; Miller & Cohen, 2001). Engaging conscious cognitive resources would logically require the sacrifice of other processes, leading to an opportunity cost of cognitive control (Kurzban, Duckworth, Kable, & Myers, 2013). A further opportunity cost that may be associated with cognitive effort include patterns of reciprocal inhibition associated with attentional engagement given in a specific domain (e.g., during visual attention tasks an individual must inhibit auditory processing) (REF).

Empirically, cumulative time-on-task has been shown to be the best predictor of phenomenological effort and fatigue, even when engaging effortful resources on differing subsequent tasks (Benoit et al., 2019 ; Boksem & Tops, 2008). The feeling of fatigue over subsequent tasks is explained by positing a link between the two tasks due to their monotonous or artificial nature, or due to them being part of the same

social engagement (Kurzban et al., 2013). Opportunity cost models are further supported over resource-limited models by the effect of motivation on effortful engagement. It has been shown that fatigue on a second task is reduced when it is viewed as sufficiently important (Muraven & Baumeister, 2000). Further, beliefs and perceptions can change how individuals engage in effortful tasks (O'Connell et al., 2007), as can how the task or reward is framed (Chow, Kohlmeyer, & Wu, 2007; Drake & Kohlmeyer, 2010; Hartman & Slapničar, 2015; Ruchala, 1999; Sprinkle, Williamson, & Upton, 2008).

However, while opportunity cost models may account for the motivational aspects of cognitive effort in choice tasks better than resource-limited models, they do not provide a comprehensive account of effortful behaviour. First, opportunity costs may not be applicable to physical effort, which has direct resource-limited effects due to the depletion of ATP in the muscles being used (Boska, 1994; Jeneson, Westerhoff, Brown, Van Echteld, & Berger, 1995; Potma, Stienen, Barends, & Elzinga, 1994; Russ, Elliott, Vandenborne, Walter, & Binder-Macleod, 2002; Szentesi, Zaremba, van Mechelen, & Stienen, 2001). In a similar vein, opportunity cost models primarily focus on explaining task choice (Kurzban, 2016), while resource-limited models focus on explaining resource allocation or disengagement during periods of sustained effortful engagement (Gailliot & Baumeister, 2007). The outcomes and behaviours relating to each model of cognitive effort are therefore fundamentally distinct, meaning the models may not be directly comparable. This distinction also relates to the stages posited by the Rubicon model of action (see section 1.2.1), as opportunity costs disappear during implementation stages of decision making, so opportunity-cost models cannot account for effortful behaviour occurring in these stages. Further, cognitive fatigue seems to be an unavoidable consequence of sustained effortful

engagement, which suggests some sort of depletable resource is associated with this action, as fatigue carries on across different effortful tasks.

Overall, there is insufficient evidence to conclusively account for the costly and fatiguing nature of cognitive effort. While resource-limited models appear intuitive, they cannot account for the motivational aspects of cognitive effort and have failed to identify a satisfactory resource which is depleted during effortful engagement. In contrast, opportunity cost models are better at explaining the motivational aspects of cognitive effort. However, opportunity cost models focus specifically on choice behaviour and may lack generalisability to sustained effortful engagement. Researchers investigating cognitive effort should be aware of resource-limited and opportunity cost models of cognitive effort when considering the theoretical implications of their experimental results.

1.1.5 Real-world implications of cognitive effort

The decision to expend effort can impact numerous diverse outcomes, such as economic decision-making, the symptoms of various clinical disorders, and becoming costlier with age.

Effort-based decision-making has also been implicated in changes in consumer behaviour (Baumeister, 2002; Clarke & Belk, 1979). A person's willingness to exert effort is closely related to how likely they are to buy different products (Steenkamp & Baumgartner, 1992), and the amount of effort consumers are willing to expend can be modulated by changing their attitude, time availability, and product knowledge (Beatty & Smith, 1987; Steenkamp & Baumgartner, 1992).

Cognitive effort seems to be a central dimension of mental illness and other clinical disorders. A lack of cognitive effort has been implicated in the symptomology

of clinical conditions including depression (Cohen, Lohr, Paul, & Boland, 2001; Hammar & Ardal, 2009; Hartlage, Alloy, Vázquez, & Dykman, 1993; Treadway, Bossaller, Shelton, & Zald, 2012; Zakzanis, Leach, & Kaplan, 1998), ADHD (Volkow et al., 2011), Parkinson's disease (Manohar et al., 2015; Sinha, Manohar, & Husain, 2013), and schizophrenia (Culbreth, Westbrook, & Barch, 2016; Fervaha, Foussias, Agid, & Remington, 2013; Gold et al., 2013; Gold, Waltz, & Frank, 2015). It is thus critical to identify the mechanisms of cognitive effort valuation as a first step toward targeted clinical interventions that address impaired cognitive motivation.

Similarly, older adults find cognitive effort to be more costly and, unlike delay discounting, this has not been found to be due to differences in income (Hess & Ennis, 2012; Westbrook et al., 2013). Differences in effortful aversion with age could be explained by dopaminergic function during reward anticipation (Mohr, Biele, & Heekeren, 2010), which is diminished in older adults and related to the invigoration of motor behaviour (Salamone, Correa, Farrar, & Mingote, 2007; Walton et al., 2006). Alternately, increased phenomenological effort in older adults may be the result of diminished executive function (Braver, 2008; Park, 2009), meaning that older adults may compensate by recruiting a greater fraction of their cognitive control resources (Park & Reuter-Lorenz, 2009).

It is often tempting for researchers investigating cognitive effort to consider it in theoretical terms alone. The broader implications of research investigating effort-based decision-making should also be assessed to understand the real-world implications of research investigating cognitive effort.

1.2 Activation and Inhibition Models of Emotion and Motivation

1.2.1 Emotion and motivation

Since cognitive effort entails an inherent conflict between an anticipated gain resulting from the completion of an effortful task, and the effort-costs of the task (Westbrook & Braver, 2015), this section will analyse the effects of losses and rewards on motivated behaviour.

Organisms are generally considered to be biologically programmed to maximise reward and minimize punishment (Guitart-Masip, et al., 2012), with the desire to avoid negative outcomes usually surpassing the desire to pursue positive ones (Tversky & Kahneman, 1991). To pursue this goal, organisms may use either hard-wired emotional responses to stimuli, such as a startle response to unexpected stimuli, or flexible top-down controlled responses based on predicting the contingent consequences of behaviour (Dickinson & Balleine, 2000; Rodríguez-Gómez, Pozo, Hinojosa, & Moreno, 2019). Emotional and top-down mechanisms usually behave in compatible ways but can come into conflict in certain situations, such as when an individual is pursuing a larger, delayed reward over a more immediate, but smaller one (Boureau & Dayan, 2011).

The emotional response to a stimulus can motivate actions ranging from basic reflexes (Lang, 1995) to complex decision-making (March, 1978). Emotional responses are posited to be unconditioned, as supported by the observation that new-borns evidence defensive (e.g., oral rejection) and appetitive (e.g., sucking) reflexes (Campos, Bertenthal, & Kermoian, 1992). Several theorists have further advocated that evolutionarily adaptive behaviour occurs along a two-phase process stemming from centrally organised appetitive and defensive motivational systems (Davidson, Ekman, Saron, Senulis, & Friesen, 1990; Dickinson & Dearing, 1979; Konorski, 1967;

Lang, 1995), mediated through specific, largely subcortical, neural circuits (Davis, 1989; Fanselow, 1994; LeDoux, 1997).

Since the nineteenth century, there has been a general consensus that the basic organisational dimensions of an organism are pleasure and arousal. At the time, approach responses were associated with pleasant stimuli and avoidance responses with unpleasant stimuli, and the intensity of the stimulus was associated with the arousal it causes (Dickinson & Dearing, 1979; Konorski, 1967; Schneirla, 1959). Arousal, defined as the state of being alert or active and its associated psychological processes (Russell, 2003), is required to react appropriately to both highly appetitive and aversive stimuli. States of both extreme inhibition and activation require high arousal, as both require high states of alertness to produce appropriate behaviour. Arousal can therefore be seen as being distinct from, but fundamentally linked to, cortical or motor activation and inhibition. This forms a 'U-shaped' relationship between the pleasantness of the stimulus and the arousal or motivation associated with it, where highly pleasant or unpleasant stimuli cause high levels of arousal or motivation, but a stimulus which is neither pleasant nor unpleasant causes little arousal or motivation. This curve is also skewed towards unpleasant stimuli, which tend to be more salient and motivating than equivalent pleasant stimuli (Taylor, 1991; Tversky & Kahneman, 1991).

Supporting biphasic conceptualisations of behaviour, multivariate studies have shown that the principal variance in emotional meaning is accounted for by pleasure and arousal (Mehrabian & Russell, 1974; Osgood, 1952), and judgements of valence and arousal covary systemically with the biological resources associated with the activation of appetitive and defensive motivational systems (Bradley & Lang, 2000; Greenwald, Cook, & Lang, 1989; Lang, Greenwald, Bradley, & Hamm, 1993).

Additionally, factor analyses consistently find that hedonic value and intensity account for most of the variability in emotional judgements (Mehrabian, 1970; Osgood, 1952; Osgood, Suci, & Tannenbaum, 1957).

More recently, the view of emotion has been described in terms of inhibition and activation rather than arousal, as an individual may be aroused while either inhibiting or activating a response (Lang, Bradley, & Cuthbert, 1997; Lang & Cuthbert, 1990). A relationship between separate appetitive and aversive stimuli is described, with responses being reciprocally inhibited, meaning that activity in one system increases as the other is inhibited (Krank, 1985). Cacioppo and Berntson (1994) advocated for a more flexible model of biphasic activation, where the reciprocity of inhibition can vary along a spectrum ranging from fully reciprocally inhibitive to fully reciprocally activating, as the co-activation of approach and avoidance tendencies may occur in response to multiple independent stimuli.

However, responses to stimuli may be more complex than described in models positing a single response to appetitive or aversive stimuli. In animal studies, reflex responses withdrawing from aversive stimuli have been shown to be ordered sequentially based on their immediacy and proximity, beginning with a freezing or fleeing response, then to information gathering, and finally to increased alertness based on the intensity of the stimulus shown (Bradley, Codispoti, Cuthbert, & Lang, 2001). The order of defensive responses also shows similarities in humans (Lang et al., 1997), with aversive stimuli causing a series of autonomic responses similar to the response of prey animals viewing a predator from afar (Bradley et al., 2001).

The defence cascade model (Bradley et al., 2001; Lang et al., 1997) states that defence responses cascade through several layers of perceptual processing, from pre-encounter to post-encounter, and finally to overt action. The pre-encounter stage is

characterised by the facilitation of perceptual processing, with classical physiological indices of orienting being found, including cardiac deceleration (Graham, 1979), moderate electrodermal increases (Vasey & Thayer, 1987), and relative inhibition of the probe startle reflex (Bradley et al., 2001). With more pronounced activation, the defensive response moves to the post-encounter stage, where oriented attention starts to give way to the metabolic mobilization needed for active defence and sympathetic reflex innervation (Bradley et al., 2001), as signalled by greater electrodermal activation and the startle response becoming potentiated (Bradley & Lang, 1999; Vrana, Spence, & Lang, 1988). The pre- and post-encounter stages are considered as motivational priming for overt action in response to the aversive stimuli (Lang et al., 1997), which can be summarised as selecting either a fight or flight response (Bradley et al., 2001).

Many investigators have discussed the interactions between appetitive and aversive neural systems during decision-making (Amemori & Graybiel, 2012; Koob & Le Moal, 2008; Park, Kahnt, Rieskamp, & Heekeren, 2011; Talmi, Dayan, Kiebel, Frith, & Dolan, 2009). Midbrain dopaminergic systems and their projection sites in the striatum have been specifically implicated in appetitive processing (Delgado, 2007; Haber & Knutson, 2010; O'Doherty, 2004; Schultz, Tremblay, & Hollerman, 2000), although these regions also participate in aversive processing (Bromberg-Martin, Matsumoto, & Hikosaka, 2010; Salamone, 1994). In contrast, processing in the amygdala and anterior insula has frequently been linked with aversive events and stimuli (Adolphs, Tranel, Damasio, & Damasio, 1994; Craig, 2002, 2009; Davis, Walker, Miles, & Grillon, 2010; LeDoux, 2000), but are also somewhat engaged in during appetitive processing (Everitt, Cardinal, Parkinson, & Robbins, 2003; Liu, Hairston, Schrier, & Fan, 2011; Mizuhiki, Richmond, & Shidara, 2012; Salzman,

Paton, Belova, & Morrison, 2007). The interaction between neural areas associated with appetitive and aversive stimuli (Choi, Padmala, Spechler, & Pessoa, 2014) suggests that these areas may instead be involved in processing motivational salience or comparing a given stimulus to an internal reference point, rather than appetite or aversion specifically (Carter, Macinnes, Huettel, & Adcock, 2009; Jensen et al., 2003; Jensen et al., 2007; Metereau & Dreher, 2013).

Historically, motivation was considered to have two separate levels; will and volition. Will was considered to encompass a person's desires and beliefs relating to a goal, representing how much they want the outcome they are working towards, and their beliefs regarding whether it is possible to achieve the goal (Pintrich, 2002). In contrast, volition was described as the actions taken to pursue a goal, including the vigour and sustainment of effortful behaviours (Kuhl, 1985). While volition and will were considered to work in concert, with volition occurring according to the strength of will, there may be situations where they may become disconnected. For example, Wolters (1998) commented on how students can express sincere desires to accomplish a goal but may have a very difficult time managing the competing goals and distractions that interfere with their academic work.

Early motivational phenomena were viewed through an action perspective, describing how the expectancy of a gain/loss leads to changes in actions pursuing a goal (Atkinson, 1957; Festinger, 1942; Lewin, Dembo, Festinger, & Sears, 1944). It was not until the emergence of the psychology of goals that the process and potential strategies received attention (Klinger, 1977; Kuhl, 1985; Wicklund & Gollwitzer, 2013), in concert with the actions taken to pursue the goal.

The motivation psychology of action focuses on questions of action control, as a strong motivation to achieve a certain outcome is not always sufficient for that

behaviour to be implemented and the goal realised (Gollwitzer & Bargh, 1996; Heckhausen & Gollwitzer, 1987; Kuhl, 1985). This conception postulates that behaviour potential is a function of perceived goal importance (value) combined with the expectancy of the probability of achieving the goal (expectancy) (Kuhl, 1985). However, while this is an important conception of motivated action, it mostly explains how people choose to pursue a specific goal (Kuhl, 1985), rather than the effort employed to pursue, in which implementation intentions (Gollwitzer, 1999) and self-regulation (Zimmerman, 2013) are also relevant.

The Rubicon model of action (Gollwitzer & Bargh, 1996) was formulated to explore the transition from goals to action by describing motivated actions as occurring across four distinct phases, existing along a temporal path, starting with a person's desires and ending with the evaluation of the action outcomes achieved (Gollwitzer, 1990; Heckhausen & Gollwitzer, 1987).

In the first phase of this model (the pre-decisional phase) the individual must identify and compare potential outcomes, but still remain uncommitted to pursuing any single goal. When the individual commits to pursuing a single goal, they enter the committed stage, where they anticipate and plan future actions to pursue their selected goals. It is during the committed stage that individuals are described as 'crossing the Rubicon' as they become committed to pursuing a single goal and therefore inhibit other potential outcomes as distractions. Once they are fully committed, the individual enters the volitional stage, which covers any self-regulatory activities engaged to initiate and sustain goal-seeking behaviours. Finally, once the individual has achieved their goal, they enter the post-actional stage, where they reflect on their actions during the previous stages and conduct a self-evaluation of the outcomes reached.

The major innovation of the Rubicon model of actions was to define clear boundaries between motivational and volitional action phases, with three clear boundaries existing at the transition between the phases described in the model. The Rubicon model of action is therefore able to distinguish between the selection of goals, the pursual of goals, and the evaluation of goals once they have been achieved. This is important when considering effortful behaviour, as decisions regarding the deployment and sustaining of effortful resources may be different depending on the stage of actions they exist within. For example, choice tasks are often used to infer individual effort-discounting rates, which exist in the pre-decisional phase; while measures of effortful performance measure engagement, existing in the volitional phase of the Rubicon model of action; and self-report measures of effort exist in the post-actional stage. It is therefore important for researchers to be aware of the stages that their measures of effort exist upon when interpreting their results.

The Rubicon model has been updated when considering the mindsets associated with each stage posited in the theory, forming the mindset theory of action (Gollwitzer, 1990), where each phase is proposed to be associated with a distinct mindset (Gollwitzer, Heckhausen, & Steller, 1990; Gollwitzer & Keller, 2016; Heckhausen, 1987). A deliberate mindset is associated with the pre-decisional phase and involves being open to multiple options and flexible to changing your mind when presented with new information. In the pre-actional phase, an individual is likely to enter an implemental mindset, where they become receptive to information that facilitates the initiation of goal-oriented behaviour, while inhibiting any information that may interfere with the initiation of goal-oriented behaviour. For this reason, individuals in this mindset are more closed-minded to new information when compared with the deliberative mindset. The mindset associated with the volitional

phase is the actional mindset, where individuals are highly focused on executing the behaviours required to achieve their goal, possibly even reaching a state of 'flow' (Wicklund & Gollwitzer, 2013). Finally, during the post-actional phase, a person may enter an evaluative mindset, as they are required to be primarily concerned with the quality of the outcome achieved, improving behaviour when selecting and choosing future outcomes.

Research on the mindset theory of action has predominantly targeted the pre-decisional and pre-actional phases, therefore analysing the features of the deliberative and implemental mindsets respectively (Heckhausen & Gollwitzer, 1987; McCrea & Vann, 2018). Further, because of their trans-situational stability, indexing action-phase related mindsets can be used to instigate behavioural change (Gollwitzer, 2012; Gollwitzer & Keller, 2016), such as showing more open mindedness in the pre-decisional phase (Fujita, Gollwitzer, & Oettingen, 2007), and more closed-mindedness during later phases (Bayer & Gollwitzer, 2005). It has also been showed that individuals with an implementational mindset often show higher persistence in the face of difficulties when compared to a deliberative mindset (Brandstätter, Giesinger, Job, & Frank, 2015) but exhibit poorer information processing and visual attention (Büttner et al., 2014). Participants in an implementational mindset are also more confident in their self-report of performance in a general knowledge test (Hügelschäfer & Achtziger, 2014) and are better shielded from the detrimental effect of the stereotype threat (Dennehy, Ben-Zeev, & Tanigawa, 2014).

The differences in mindsets associated with each stage of the Rubicon model of action further highlight the importance in considering the stage at which effortful behaviour occurs. The behaviour made and individual differences between effort-based decision-making may be significantly different depending on the stage it occurs

due to the biases and behaviour associated with each mindset. For example, if participants are informed of a monetary loss associated with an outcome during the pre-decisional phase, they are likely to be more open to this information, whereas if they are presented with this information during a volitional phase, they may be more likely to ignore or disregard it.

Most theories of motivation assume that goal characteristics or individuals' need states are crucial in resource deployment (McClelland, Atkinson, Clark, & Lowell, 1953; Wigfield & Eccles, 2000). However, motivational intensity theory (Richter, 2015; Brehm, & Self, 1989; Gendolla, Wright, & Richter, 2012; Michael Richter, 2013; Wright, 2008; Wright & Pantaleo, 2013; Richter, Gendolla, & Wright, 2016) postulates that resource mobilization follows a "difficulty law of motivation" (Hillgruber, 1912), meaning that effort is mobilized proportional to the difficulty of the task, rather than the SV of associated incentives. Motivational intensity theory is grounded in energy conservation, which predicts that individuals mobilize effortful resources only to the degree needed to attain the goal, and only when the benefits associated with the action outweigh its potential costs. Expected benefit should only modulate the deployment of effortful resources indirectly, by setting an upper limit to the potential amount of resources deployed to seek a goal (Kruglanski, Chernikova, Rosenzweig, & Kopetz, 2014). However, in situations where the difficulty of the task is unclear, motivational intensity theory posits that effortful resources are deployed proportional to potential motivation, so the resources deployed do not outweigh the potential benefit (Brehm & Self, 1989; Gendolla, Brinkmann, & Silvestrini, 2012; Richter, 2013, 2015; Richter, Friedrich, & Gendolla, 2008; Wright & Kirby, 2001; Wright, 1996; Wright, 2008).

Most research on effort mobilization conducted in the context of motivational intensity theory has measured effortful deployment using CV indicators or through the measurement of grip force. The sympathetic nervous system, reflected in CV indicators (e.g., systolic blood pressure, cardiac pre-ejection period), responds when individuals are actively engaged in the mobilization of effortful resources, and is generally considered to reflect effortful engagement (Newlin & Levenson, 1979; Obrist, 2012; Segers, Steendijk, Stergiopulos, & Westerhof, 2001; Wright, 1996). A large number of CV studies have been conducted testing the basic predictions of motivational intensity theory, showing task difficulty primarily effects sympathetic responses rather than success importance (Brinkmann & Gendolla, 2008; Freydefont, Gendolla, & Silvestrini, 2012; Gendolla, 2012; Gendolla & Krüsken, 2002; Gendolla & Richter, 2006; Richter, Baeriswyl, & Roets, 2012; Wright, Murray, Storey, & Williams, 1997; Wright, Shaw, & Jones, 1990; Wright, Williams, & Dill, 1992), and that the sympathetic nervous response increases with difficulty, but not when the task becomes impossible (Richter 2008; Wright 1990).

In contrast, research using force grip measurements has found mixed results regarding the predictions of the motivational intensity theory. The muscle force exerted in isometric tasks acts proportional to the amount of ATP that is used for muscle contraction (Boska, 1994; Jeneson, Westerhoff, Brown, Van Echteld, & Berger, 1995; Potma, Stienen, Barends, & Elzinga, 1994; Russ, Elliott, Vandenborne, Walter, & Binder-Macleod, 2002; Szentesi, Zaremba, van Mechelen, & Stienen, 2001). Given that ATP is the primary fuel of muscle contraction, assessing the force exerted in such tasks provides information about the amount of resources invested, allowing for the testing of the resource conservation principal posited by motivational intensity theory (Richter et al., 2016). However, studies conducted using force grip

paradigms have countered the resource conservation principal, showing that participants generally commit more resources than are necessary (Richter, 2015; Stanek & Richter, 2021). Further, force grip studies on the joint impact of task difficulty and success importance did not show the predicted disengagement when success importance was low, suggesting an additive effect of reward value and task difficulty rather than the predicted difficulty main-effect (Stanek & Richter, 2021).

In conclusion, organisms are biologically programmed to seek reward and avoid punishment, with positive and negative stimuli affecting arousal and motivation symmetrically, forming a 'U-shaped' curve. Cognitive effort is often conceptualised as being deployed proportional to the SV of associated incentives. However, much of this behaviour is determined by immediate appetitive and aversive responses to stimuli, with highly arousing pleasant and unpleasant stimuli inducing a cascading defensive response, potentially causing a reduction in effortful performance. The confounding factors stemming from emotion and motivation systems should be considered when investigating cognitive effort using performance-based measures.

1.2.2 Inhibition and activation models

Engaging in tasks requiring sustained cognitive effort often require balancing the processes of cortical activation and inhibition (Westbrook & Braver, 2015). Models of competing activation and inhibition should be considered when investigating the cortical basis of effortful behaviour and decisions.

The ability to inhibit a prepared movement is an important function which requires a high degree of executive action and functional integration across multiple brain regions (Nigg, 2000). The inhibition of a planned or automated action requires deliberate control of a primary motor response in compliance with updated situational cues (Nigg, 2000), as well as active control of associated neural areas (Aron et al.,

2007; Harnishfeger, 1995; MacLeod, Dodd, Sheard, Wilson, & Bibi, 2003). Cognitive control is often associated with a top-down control system, which governs the activation of task-relevant and the inhibition of task-irrelevant neural areas and cognitive schema (Norman & Shallice, 1986; Shallice, 1994). Inhibition is, therefore, closely related to cognitive effort and control, and the opportunity cost of effort may relate to the activation of task-relevant areas requiring the inhibition of irrelevant areas (Yi & Friedman, 2011).

Further, behaving in a goal-directed manner often requires the suppression of inappropriate movement tendencies (Bestmann & Duque, 2016; Luna, Marek, Larsen, Tervo-Clemmens, & Chahal, 2015), and, without the efficient operation of inhibition, control behaviour becomes maladaptive (e.g., in people diagnosed with ADHD or Tourette's syndrome, or in older individuals) (Aron & Poldrack, 2005; Bartholdy, Dalton, O'Daly, Campbell, & Schmidt, 2016; Fujiyama, Hinder, Schmidt, Garry, & Summers, 2012; Milad & Rauch, 2012; Verbruggen & Logan, 2008). For this reason, motor systems must select and execute correct responses (Logan & Cowan, 1984) while simultaneously inhibiting incorrect or inappropriate responses (Duque, Greenhouse, Labruna, & Ivry, 2017). The strategic selection of motor responses requires a rapid top-down control mechanism which interacts with slower bottom-up processes to monitor ongoing performance (Verbruggen & Logan, 2008).

However, motor actions and inhibition are better described as a mix of automatic and controlled responses (Andres, Guerrini, Phillips, & Perfect, 2008; Collette, Schmidt, Scherrer, Adam, & Salmon, 2009; Friedman & Miyake, 2004; Ludowig et al., 2010; Piai, Roelofs, & van der Meij, 2012). Automatic behaviours are rapid, smooth, effortless and require no conscious monitoring, whereas conscious processes are flexible, but effortful and require conscious monitoring (Evans, 2008;

Kahneman, 2011; Sloman, 1996). Automatic behaviours are useful for controlling simple, universal actions or inhibitions, whereas conscious behaviours are useful for controlling actions in complex tasks, or tasks with unexpected events.

Similar to the distinctions between conscious and automatic inhibition, many other distinctions between different forms of inhibition have been made, including motor inhibition (Robinson, Krimsky, & Grillon, 2013), lateral inhibition (Bridgeman, 2006), pre-pulse inhibition (Dawson, Oray, Lu, & Schell, 2004), the inhibition of return (Possin, Filoteo, Song, & Salmon, 2009), knowledge or semantic inhibition (Debruille, 1998), and proactive interference (Yi & Friedman, 2011).

Distinctions have also been made between active and passive avoidance (Affandi, Pike, & Robinson, 2021; Riley & Foss, 1991). Passive avoidance occurs when an organism is required to inhibit a prepared or conditioned response, whereas active avoidance occurs when an organism is required to take active steps to avoid a threatening or aversive stimulus (Binti Affandi et al., 2021; Riley & Foss, 1991). Active and passive avoidance often result in marked differences in the levels of arousal exhibited by the organism; active avoidance is associated with an increase in arousal, whereas passive avoidance may result in signs of reduced arousal, or even freezing behaviour (Binti Affandi et al., 2021; Riley & Foss, 1991).

Alternatively, more unitary forms of inhibition have been proposed (Collette et al., 2009; Duque et al., 2017; Hasher & Zacks, 1988). A key proposition states that there are two forms of motor inhibition (Duque et al., 2017). The first is global inhibition, which acts as an ‘emergency brake’ to inhibitive stimuli, and the second is selective inhibition, which is slower and can selectively block individual responses.

Global inhibition is described as an internally generated act of control produced by higher-order executive systems (Williams, Ponesse, Schachar, Logan, & Tannock,

1999), occurring when stimuli, or stimuli perception, changes rapidly (van den Wildenberg et al., 2010). Several theoretical models have been proposed to explain the process of global inhibition, including the horse-race model of motor actions (Logan & Cowan, 1984), which posits competing activation and inhibition responses to Go and NoGo cues beginning at different time-points during a stop-signal task.

Voluntary motor actions are predominately controlled by the contralateral M1, which integrates relevant information from visual and other sensory stimuli (Stinear, Coxon, & Byblow, 2009). Alongside this, certain areas of the brainstem such as the reticular formation are related to the activation of a large group of muscles (Peterson, Maunz, Pitts, & Mackel, 1975), innervation of forearm and intrinsic hand muscles, and controlling motor activity during fine finger movements (Riddle & Baker, 2006).

Conversely, inhibition of motor responses has commonly been associated with the right IFC (Aron, Robbins, & Poldrack, 2014; Cai, Ryali, Chen, Li, & Menon, 2014; Chevrier, Noseworthy, & Schachar, 2007; Swick, Ashley, & Turken, 2011), which is found to be critical in stopping behaviour (Aron, Dowson, Sahakian, & Robbins, 2003; Sakagami, Pan, & Uttl, 2006). The IFC is thought to send inhibitory signals to motor areas (Garavan et al., 2006), or subcortical motor structures, such as the STN of the basal ganglia (Aron, 2007). The right IFC may function by blocking motor responses as they pass through the basal ganglia (Eagle & Robbins, 2003; Rieger, Gauggel, & Burmeister, 2003), in particular the STN (Aron & Poldrack, 2006; Coxon, Stinear, & Byblow, 2006; Eagle, Bari, & Robbins, 2008; Kuhn et al., 2004; van den Wildenberg et al., 2006).

The deployment of effortful resources is described in opportunity cost models as being the result of patterns of strategic activation and inhibition. This occurs due to reciprocal inhibition associated with task-relevant activation (e.g., inhibiting auditory

processing during a visual attention task) causing an inherent opportunity cost. Common measures of effortful performance, such as response-speeds and NoGo stopping rates may also involve a combination of motor activation and inhibition. The patterns of cortical activation and inhibition associated with RT and Go/NoGo tasks should therefore be considered when investigating the cortical underpinnings of effortful performance.

1.2.3 Horse-race model of motor actions

As a leading model in the understanding of motor behaviour and inhibition, the horse-race model of motor actions was developed to bridge the gap between motor inhibition and cognitive control (Logan & Cowan, 1984). This model focuses on the interactions between an executive system, which forms intentions and issues commands to realise the intentions of the actor, and a subordinate system, which interprets and carries out intentions and commands.

Opposing processes of motor activation and inhibition occurring when participants are presented with stop signals are posited by the horse race theory of motor actions (Band & Logan, 2003; Logan & Cowan, 1984; Schultz, 2015). The process of motor activation responds as quickly as possible to a Go cue, controlling the RTs of the primary task demands. Then, the process of motor inhibition occurs in response to the stop-signal, cancelling the earlier prepared movement. In this model, a prepared movement is successfully inhibited if the inhibitive process completes before the movement process, meaning a successful inhibition response to stop-signals is based on the relative speed of the competing processes, rather than their strength (Band & Logan, 2003). Deficiencies in stopping may occur when the stop-signal is not detected, or not translated into an internal command (Band & Logan, 2003).

The horse-race model of motor actions is a key model in the understanding of inhibitory control, positing separate and competing inhibition and activation processes. This may be important in understanding the implementation of cognitive control, which may be necessary to select between the competing activation and inhibition processes, and the neural underpinnings of these processes should be further investigated. The horse-race model of motor actions is also useful when accounting for inhibition functions, meaning it can be used to successfully predict the primary task error-rate, signal-response RTs, and stop-signal RTs (Logan & Cowan, 1984). The stop-signal RT remains relatively constant, at around 200 ms, for a range of inhibitive functions including continuous actions (e.g., typing) (Logan, 1986), as well as the inhibition of learned responses (Logan & Cowan, 1984).

The horse-race model of motor actions is used as a theoretical background for the consideration of motor action and inhibition observed during the RT and Go/NoGo tasks used in the present thesis. Specifically, the competing processes of activation and inhibition described by the horse-race model of motor actions were observed in the research paper discussed in chapter 4, with differing patterns of cortical activation and inhibition occurring depending on the task structure employed..

1.3 Decision-Making

1.3.1 Neuroeconomics

Neuroeconomics is a relatively new field of scientific research investigating the neural regions underlying the calculation of SVs during decision-making, as well as the discounting effects of various economic factors (Bossaerts & Murawski, 2015; Glimcher, 2004; Konovalov & Krajbich, 2019). The following chapters will discuss the discounting effects associated with effort, reward probability, and reward delay, as well as the differences in SV associated with monetary gains and losses.

1.3.1.1 Prospect theory

Prospect theory is a non-axiomatic theory of decision-making that posits two decision-making functions; a utility function and a probabilistic weighting function (Levy, 1992), formulated to provide a more comprehensive account of how individuals make probabilistic decisions under losses and gains (Kahneman & Tversky, 1979; Tversky & Kahneman, 1992). In prospect theory, individuals are posited to evaluate outcomes with respect to a reference point rather than absolute value, give more weight to losses and comparable gains, and are generally risk-averse with respect to gains and risk-seeking with respect to losses (Kahneman & Tversky, 1979; Tversky & Kahneman, 1992).

The main features of prospect theory are that it posits a utility function that is steeper for losses than gains and describes choices as being made using a two-phase process: editing and evaluation. During the editing phase of the decision-making process, the decision-maker is posited to simplify the outcomes of the choice by creating representations of the choices that will be passed onto the next phase, where similar outcomes are combined and differing outcomes are separated (Wilkinson & Klaes, 2012; Glimcher & Fehr, 2014). Following the editing phase is the evaluation phase, where all outcomes are compared in the evaluation phase and the prospect offering the highest SV is chosen.

The shape of the utility function posited in prospect theory describes the observation that individuals show increased sensitivity to losses compared to gains of equal nominal value, or are generally loss averse, manifested in the steeper slope of the value function in the loss compared to the gain domain (Kahneman, Knetsch, & Thaler, 1991).

1.3.1.2 Loss Aversion

Consistent with the asymmetric slopes of the utility function in the loss and gain domains in prospect theory, a classical finding in psychological research is that negative events are more attention-grabbing and influential than their positive counterparts (Baumeister et al., 2001; Rozin & Royzman, 2001). Humans show profound asymmetries in their subjective responses to gains and losses, such as when incentivised with a monetary reward compared to threatened with a monetary loss (Baumeister et al., 2001; Rozin & Royzman, 2001; Vaish, Grossmann, & Woodward, 2008). Loss aversion was created to describe this asymmetry, stating that outcomes framed as losses carry more subjective weight than outcomes framed as gains (Kahneman & Tversky, 1979). Losses have also been shown to cause more physiological arousal, as indexed by larger pupil diameters and higher heart-rate (Hochman & Yechiam, 2011; Low, Lang, Smith, & Bradley, 2008; Satterthwaite et al., 2007), increased attention (Yechiam & Hochman, 2013), and increased activation in frontal and striatal regions of the brain (Gehring & Willoughby, 2002; Holroyd & Coles, 2002; Sokol-Hessner, Camerer, & Phelps, 2013; Tom, Fox, Trepel, & Poldrack, 2007; Yeung, Botvinick, & Cohen, 2004).

Conversely, several more recent studies have found no loss aversion in tasks measuring the maximum amount an individual would be willing to pay to secure an option (Abdellaoui, Bleichrodt, & Paraschiv, 2007; Ert & Erev, 2013; Rozin & Royzman, 2001; Walasek & Stewart, 2015; Yechiam & Hochman, 2013). This has led to the suggestion that loss aversion may be observed only in specific contexts (Ert & Erev, 2013; Gal & Rucker, 2018), or that it does not exist as an independent phenomenon (Yechiam & Hochman, 2013).

However, while studies have found inconsistent results regarding loss aversion, it is a common finding that losses are associated with increased arousal and attention compared to gains of equal nominal value (Hochman, Glöckner, & Yechiam, 2009; Hochman & Yechiam, 2011; Satterthwaite et al., 2007; Taylor, 1991). Similarly, unpleasant compared to pleasant events tend to evoke more attention, as well as stronger and longer-lasting changes in mood and emotion (Baumeister et al., 2001; Rozin & Royzman, 2001; Taylor, 1991).

Based on these findings, Yechiam and Hochman (2013) developed the attention-based view of losses as an alternative to the concept of loss aversion posited by Kahneman and Tversky (1979). The attention-based view of losses breaks with previous conceptions of loss aversion by positing that losses are not more subjectively valuable than gains, but are only more salient, leading to an attentional orienting response, causing the illusion of loss aversion in certain circumstances (Yechiam & Hochman, 2013). For example, in loss trials during choice tasks participants may be more focused on the potential loss associated with a choice over other features of the choice (e.g., delay or effort requirements). This account also points to the idea that COGED tasks may not directly measure effort-discounting rates and may be confounded by factors such as stimulus saliency, including the valence of the reward or how visually salient the choice is (e.g., word colour or size).

While often being used to pursue a potential reward, cognitive effort may also be implemented to avoid being punished. However, the implementation of cognitive effort under losses and gains may have marked differences, both because losses are more motivating than gains (Baumeister, Bratslavsky, Finkenauer, & Vohs, 2001; Rozin & Royzman, 2001), and because losses and gains have different effects on the implementation of cognitive resources (Boksem, Tops, Kostermans, & De Cremer,

2008; Maruo, Schacht, Sommer, & Masaki, 2016; Seifert, Naumann, Hewig, Hagemann, & Bartussek, 2006).

Cognitive effort is considered using neuroeconomic conceptions in the present thesis, specifically as a discounting factor and as being deployed relative to the SV of offered incentives. The theoretical basis of neuroeconomics and loss aversion should therefore be considered to provide a comprehensive interpretation of the research presented.

1.3.2 Reward discounting

When choosing between two amounts of the same reinforcer, organisms will generally prefer the option offering the larger amount (Catania, 1963; Neuringer, 1967). However, there are scenarios where organisms will pursue a smaller reinforcer (Kendall, 1974), such as if the reward is associated with a temporal delay (Green & Myerson, 2004; Rachlin & Green, 1972), has only a limited probability of being received (Green & Myerson, 2004), or requires the engagement of cognitive or physical effort (Jones & Rachlin, 2006; Nishiyama, 2014; Sugiwaka & Okouchi, 2004). In the following section, **t**he interactions between discounting factors and the discounting effects of probability and delay will be discussed.

Cognitive effort is conceptualised as a discounting factor in the present thesis, deployed proportional to the SV of associated incentives. It is therefore important to consider the neuroeconomic basis of reward discounting, and to compare effort-based discounting to other discounting factors such as probability and delay.

1.3.2.1 Effort discounting

Due to its aversive nature, effort can be conceptualised in economic terms as a discounting factor, which reduces the subjective value of prospective rewards (Walton,

Kennerley, Bannerman, Phillips, & Rushworth, 2006; Prevost, Pessiglione, Metereau, Clery-Melin, & Dreher, 2010), similar to the discounting effect of probabilistic (Rachlin, Raineri, & Cross, 1991) and delayed rewards (Kirby, 2009).

Conceptualising effort in economic terms allows it to be investigated using decision-making paradigms (Bialaszek, Marcowski, & Ostaszewski, 2017; Mitchell, 2004; Sugiwaka & Okouchi, 2004; Westbrook, Kester, & Braver, 2013). The intuitive link between the implementation of effort and reward has been investigated using behavioural and economic accounts of decision-making (Walton et al., 2006). For example, the COGED paradigm has been used to describe and compare the discounting functions associated with effort requirements and incentive delay, where the underlying activation associated with these discounting effects (Massar, Libedinsky, Weiyan, Huettel, & Chee, 2015).

The rates of differing discounting factors can be modelled using discounting curves across multiple levels of reward. An example of changing discounting rates across reward levels is the amount effect, where larger effortful or delayed rewards are discounted less steeply than smaller rewards (Green & Myerson, 2013; Kirby, 1997; Thaler, 1981; Ostaszewski et al., 2013; Bialaszek et al., 2017; Białaszek et al., 2019). However, in regards to probabilistic rewards, a reverse amount effect is commonly found, where larger probabilistic rewards are discounted more steeply than smaller rewards (Green, Myerson, & Ostaszewski, 1999; Myerson, Green, & Morris, 2011).

Differing discounting factors can also be compared using correlations across participants, or the way discounting factors interact when compared with the same reward can be investigated.

1.3.2.2 Probability discounting

Probability discounting relates to the observation that, when faced with an uncertain outcome, individuals will discount the subjective value of a reward in proportion to the probability of receiving it (Rachlin, 2006). The probability discounting rates of individuals can be assessed using discounting procedures, where steeper discounting curves indicate that an individual tends to make decisions favouring smaller, but higher-probability outcomes (Rachlin, 2006).

In existing research, probability discounting curves are widely fitted to exponential and hyperbolic models. Several studies have compared the goodness of fit of differing models in relation to probabilistic monetary outcomes, indicating that hyperbolic models fit individuals' discounting rates better than exponential models (Rachlin et al., 1991; Richards, Zhang, Mitchell, & de Wit, 1999). Hyperbolic models have also been fitted to the probability discounting of other rewards, such as consumable goods or environmental outcomes (Chen, Chen, Wang, & He, 2019).

A third method has been proposed to model probability discounting curves using an additive-utility model (Killeen, 2009, 2015). The additive utility model works by adding the subjective utilities of outcome and probability, regarding probability as a disutility rather than a discounting multiplier. In support of this model, Doyle and Chen (2010) and Doyle and Chen (2012) conducted a meta-analysis on the probability discounting curves of several studies and found that the additive-utility model provided a better goodness of fit than either the exponential or hyperbolic models.

Overall, the discounting rates of probability show some similarities to those of effort-based discounting, as both form a hyperbolic curve, with amounts added being stronger when the reward is lower compared to when it is larger. There are, however, some key differences between the two, and understanding the basis of these differences

could improve understanding of how people make decisions regarding rewards discounted by both probability and effort.

1.3.2.3 Delay discounting

Delay discounting refers to the observation that, when humans are offered a choice between equivalent rewards, they will usually devalue outcomes proportional to the length of time they would have to wait before receiving them (Kirby, 2009). Alterations in delay discounting have been observed in conditions such as pathological gambling (Dixon, Marley, & Jacobs, 2003), substance abuse (Yi, Mitchell, & Bickel, 2010), and ADHD (Wilson, Mitchell, Musser, Schmitt, & Nigg, 2011).

An individual's propensity to devalue delayed rewards can be investigated using delay discounting tasks (Madden & Bickel, 2010), which require participants to choose between a smaller, immediate reward, and a larger, delayed reward. The amount offered for the immediate reward is adjusted following a staircase procedure depending on participant choice. Then, over a series of repeated choices, an indifference point can be established as an estimate of individual subjective values over different lengths of delay.

During discounting tasks, indifference points tend to become smaller as delay increases, and this can be described using a hyperbolic or additive-utility model (Doyle & Chen, 2010, 2012; Mazur, 1987), meaning that participants discount larger delayed rewards less steeply than smaller rewards (Green & Myerson, 2013; Kirby, 1997; Thaler, 1981). The amount effect is found not just for monetary rewards, but also with outcomes such as health (Chapman, 1996), and consumables (Estle, Green, Myerson, & Holt, 2007; Raineri & Rachlin, 1993).

There are two hypotheses designed to explain delay discounting. The first describes delay discounting as resulting from the interaction between two competing

neural systems, the first being specialised to value immediate rewards and the second being specialised to value delayed rewards (McClure, Laibson, Loewenstein, & Cohen, 2004). In contrast, the second describes a single neural system which values both immediate and delayed rewards, then selects the preferable option (Kable & Glimcher, 2007). The single system account seems to be the most well supported explanation of delay discounting, although the debate is still ongoing and further research is required (Lebreton, Jorge, Michel, Thirion, & Pessiglione, 2009).

The tendency to have a preference or aversion towards delayed rewards is often considered to be an individual personality trait (Odum, 2011). This idea is supported by evidence showing that this tendency develops with maturity, remains stable over time, and is highly heritable (Odum, 2011). In line with this interpretation, delay discounting is considered to be a direct measure, or as least a strong expression, of the personality trait impulsivity (Madden & Bickel, 2010), although evidence supporting this idea is somewhat mixed (Ainslie, 1975; Gianotti, Figner, Ebstein, & Knoch, 2012; Kirby, Petry, & Bickel, 1999; Monterosso & Ainslie, 1999; Reynolds, 2006). Further, this proposal may be rather simplistic, as impulsivity is a multidimensional concept that comprises a range of stable individual factors such as deficits in inhibitory control (Logan & Cowan, 1984), an insensitivity to delayed consequences (Ainslie, 1975; Madden & Bickel, 2010), or a tendency towards risk-taking (Green & Myerson, 2013).

In conclusion, delay discounting is the tendency to avoid delayed rewards over more immediate ones, and this shows similarities in shape to both probability and delay discounting, with similar amount effects to effort rather than probability discounting.

1.3.2.4 Combining discounting effects

The differing discounting effects discussed are usually considered to be independent factors in decision making. There may, however, be cases where these interact or are interdependent.

The relationship between discounting factors has most commonly been investigated using correlations between delayed and probabilistic rewards, as both are theorized to be underpinned by impulsivity (Myerson, Green, & Warusawitharana, 2001; Rachlin & Green, 1972). However, while some studies have found correlations between the individual SVs of probability and delay discounting (Kool & Botvinick, 2013; Mitchell, 1999; Richards et al., 1999), others have only found significant correlations between SVs of probability and delay in specific groups or conditions (Myerson, Green, Hanson, Holt, & Estle, 2003; Scheres et al., 2006), or no significant correlations at all (Holt, Green, & Myerson, 2003; Ohmura, Takahashi, & Kitamura, 2005; Olson, Hooper, Collins, & Luciana, 2007; Peters & Buchel, 2009; Reynolds, Richards, Horn, & Karraker, 2004; Weber & Huettel, 2008).

While factor analyses are well utilized in research on personality and individual differences (Russell, 2003), only a few studies have investigated the underlying factors behind the SVs of different discounting types. For example, Green and Myerson (2013) showed that the delay and probability discounting of food and money were loaded onto two separate factors, related not to the outcome, but rather to the discounting effects. In contrast, other studies have suggested that individual differences in probability and delay discounting may instead be outcome specific, although these studies did not investigate the two discounting factors together (Terrell, Derenne, & Weatherly, 2014). Tying this research together, Białaszek, Ostaszewski, Green, and Myerson (2019), examined the similarities between delay, effort,

probability, and social discounting using correlations and factor analyses. The research showed that there is an underlying factor behind the discounting of large against small rewards, and that there are correlations between delay and effort discounting.

Further, while the discounting factors of delay, effort, and probability can all be fitted to a hyperboloid function (Green, Fry, & Myerson, 1994; Green & Myerson, 2004; Green, Myerson, Oliveira, & Chang, 2013; Odum, Baumann, & Rimington, 2006), the exact shape of this function is uniquely distinguishable for each. For example, smaller rewards are discounted more steeply when delayed and less steeply when associated with probability, known as the amount effect and the reverse amount effect respectively (Green et al., 1994; Green & Myerson, 2004). Much less is known about the amount effect in regards to effort discounting, although it appears to show an amount effect is more similar to delay than probability discounting, as larger rewards are discounted less steeply when associated with the implementation of cognitive or physical effort (Bialaszek et al., 2017; Guitart-Masip, Huys, et al., 2012; Ostaszewski et al., 2013).

Variations in the SVs of discounting factors between individuals have been correlated with activation in several brain regions, including the medial PFC, the PCC & the VS (Acikalin, Gorgolewski, & Poldrack, 2017; Bartra, McGuire, & Kable, 2013; Clithero & Rangel, 2014; Kable & Glimcher, 2007; Roesch, Taylor, & Schoenbaum, 2006). However, there is evidence for regional specialisation depending on the decision factor being considered. For example, the SVs of effort are associated with significantly stronger activation in the ACC and insula compared to delay discounting (Massar et al., 2015; Prévost, Pessiglione, Météreau, Cléry-Melin, & Dreher, 2010), and significantly stronger activation in the mid-cingulate and supplementary motor area compared to probability discounting (Burke, Brunger, Kahnt, Park, & Tobler,

2013). This indicates that, while the SVs of different discounting types are associated with overlapping patterns of activation, there are key differences between the patterns of activation associated with each.

Elucidating on previous findings, Seaman et al. (2018) found that the preferences for lower physical effort, higher probability, and larger delays were uncorrelated, but all related to activation in the medial PFC, an area associated with reward valuation in both qualitative (Kable & Glimcher, 2009; Peters & Büchel, 2010), and quantitative (Acikalin et al., 2017; Bartra et al., 2013; Clithero & Rangel, 2014; Langner et al., 2014) reviews and meta-analyses. The findings of Seaman et al. (2018) further support the idea that the overlap in the neural activation associated with the SVs of different discounting types simply represent commonalities in reward processing.

An alternate way the associations between discounting effects can be considered is by investigating how they interact when associated with the same reward. A key example as to how discounting factors interact comes from the concept of probabilistic waiting, which occurs in situations where a probabilistic outcome is repeated until the reward is received (Rachlin, 1990). Probabilistic waiting, therefore, involves both a probabilistic and delayed reward. Settings with common examples of probabilistic waiting comes from real-world gambling scenarios, where gamblers routinely place bets repeatedly until a reward is received. Probabilistic waiting is, however, often conceptualised in terms of probability discounting, based on the models used to account for one-shot gambles (Holt et al., 2003; Madden, Petry, & Johnson, 2009).

The ‘string theory’ of repeated gambles posits that the subjective value of repeated probabilistic choices is based on individuals structuring the repeated choices

as a string of losses followed by a win (Rachlin, 1990; Rachlin, Safin, Arfer, & Yen, 2015; Rachlin & Siegel, 1994). The prospective value of a string of gambles is, therefore, calculated by estimating the probability of delay across all possible strings, and the discounted values are then summed and weighted against a potential reward. For example, if an individual is engaged in a series of probabilistic choices, each based on the flip of a coin, the most likely string would be an immediate win, then a loss followed by a win, then two losses followed by a win, and so on (Rachlin et al., 2015). Choices with lower probabilities are, therefore, discounted more strongly due to their anticipated delay rather than their anticipated probability (Petry & Madden, 2010; Vanderveldt, Green, & Rachlin, 2017).

A key proposal tying effort and delay discounting together comes from the opportunity cost of time, which combines the opportunity cost of expending cognitive resources with delay discounting (Otto & Daw, 2019). In this proposal, effort and delay discounting act in competition in scenarios where engaging more effortful resources mean an individual can finish a task sooner to receive a more immediate reward. The opportunity cost of time, therefore, represents a trade-off between the effort engaged in the task and the delay of the associated reward.

Investigating the interaction between effort and delay discounting using this task structure provides support for the theorised opportunity cost of cognitive effort, as there may be competing opportunity costs from both the cognitive resources employed in the task and the time it takes to complete. Otto and Daw (2019) found, in a limited stimulus detection task, that participants withheld effort when the opportunity cost of time was low and engaged effort when it was high. This supports the opportunity cost of effort by showing that cognitive control changed dynamically with

opportunity costs in a task, providing a formalized account of the opportunity costs of effort and time.

When investigating the interaction between effort and probability discounting, Kivetz (2003) found that effortful requirements enhanced participant preferences for certain but smaller rewards over larger but uncertain rewards, but that continuously increasing effortful requirements reduced this preference. This led to the observation of an 'inverted-U' effect of effortful requirements on the preference for certain rewards, with both low and high effortful requirements leading to a preference for uncertain rewards, but moderate effortful requirements leading to a preference for certain rewards. Kivetz (2003) interpreted their results as relating to the sunk-cost effect, or that engaging some effortful resources made participants less willing to lose the associated reward, but that high effortful expenditure leads them to seek a larger reward as compensation.

In conclusion, while there are many overlaps between discounting factors, especially between delay- and effort-based discounting, differing discounting factors should not be considered to be common factors in decision-making processes. Further, when different discounting factors are associated with the same reward, they may interact in complex and nuanced ways, as has been shown between delay and probability discounting, and between effort and delay discounting. The effect of probabilistic and delayed rewards on effortful engagement, however, is yet to be investigated and further research is required.

1.3.2.5 The effects of gains and losses on cognitive effort

Monetary incentives have been used to benefit response facilitation (Knutson, Fong, Adams, Varner, & Hommer, 2001; Knutson, Westdorp, Kaiser, & Hommer, 2000), attentional discrimination (Engelmann, Damaraju, Padmala, & Pessoa, 2009)

and improved cognitive control (Padmala & Pessoa, 2011). The effect of losses on cognitive effort relates to the neuroeconomic conception of effort as a discounting factor, where the effort engaged in a task should be directly proportional to the subjective value of the incentive associated with the task (Bialaszek et al., 2017; Ostaszewski, Bąbel, & Swebodziński, 2013; Sugiwaka & Okouchi, 2004). It would therefore be predicted that as losses are more motivating than gains, they should cause greater improvements in effortful performance when used as incentives.

However, studies requiring participants to engage in effortful tasks often report no significant difference in performance when participants are incentivised with equivalent losses or gains (Boksem et al., 2008; Maruo et al., 2016; Seifert et al., 2006), or even a relative deterioration in performance when participants are incentivised with losses compared to gains of equal nominal value (Hagger et al., 2010; Paschke et al., 2015; Potts, 2011). For example, Carsten, Hoofs, Boehler, and Krebs (2018) investigated the effect of gains and losses on cognitive performance during a Stroop task. RTs were found to be significantly faster when participants were incentivised with gains compared to losses, especially during congruent trials.

The leading explanation for this divergent effect is that losses cause a deterioration in effortful performance relative to gains due to the associations of positive and negative incentives to Pavlovian approach and avoidance tendencies (Chapman, Gallivan, Wong, Wispinski, & Enns, 2015; Zheng et al., 2017). In this explanation, losses cause a relative deterioration in performance because they are associated with avoidance tendencies, slowing responses, whereas gains are associated with approach tendencies, speeding responses (Chen, Lakshminarayanan, & Santos, 2006; De Houwer, Crombez, Baeyens, & Hermans, 2001; Duckworth, Bargh, Garcia, & Chaiken, 2002; Markman & Brendl, 2005; Rinck & Becker, 2007; Solarz, 1960).

While an interaction between incentive valence and approach avoidance associations would be expected (Pessoa, 2008, 2009), studies investigating this interaction during Go/NoGo tasks have reported inconsistent findings. Some research investigating the incentive valence and approach/avoidance interaction showed that gains and losses enhance approach/avoidance behaviour in trials compatible to the valence of the incentive offered (i.e., Go-gain/NoGo-loss) (Guitart-Masip et al., 2011; Guitart-Masip et al., 2012; Richter et al., 2014; Hoofs, Böhler, & Krebs, 2019). However, other research failed to find such an interaction (Boehler, Hopf, Stoppel, & Krebs, 2012; Verbruggen & McLaren, 2018; Schevernels, Bombeke, Krebs, & Boehler, 2016). There are several differences in the methodologies used which may explain this inconsistent set of findings. Firstly, early research (Guitart-Masip et al., 2011; Guitart-Masip et al., 2012) contrasted win to loss conditions, without the use of no incentive conditions, while other experiments included no-incentive trials (Schevernels et al., 2016), or contrasted win, loss, and no-incentive manipulations between groups (Verbruggen & McLaren, 2018). Consequently, early research did not contrast positive and negative stimuli to a neutral control, meaning that the difference between gains and losses may be sharper than studies with a neutral control. Secondly, research investigating the interaction between incentive valence and approach/avoidance behavioural tendencies differed regarding the response requirements used; with some comparing Go to NoGo trials (Guitart-Masip et al., 2011; Guitart-Masip et al., 2012), some comparing a Go response to the cancellation of a planned movements (Boehler et al., 2012), and others comparing approach to avoidance responses (Hoofs, Böhler, & Krebs, 2019). Thirdly, the tasks used differed in terms of their valence-action signalling, with some studies using fixed valence-action stimuli (Guitart-Masip et al., 2011; Guitart-Masip et al., 2012; Richter et al.,

2014; Schevernels et al., 2016), some using orthogonal valence-action mappings (Boehler et al., 2012; Hoofs et al., 2019), and others using group-based manipulations (Hoofs et al., 2019). Generally, trial-by-trial manipulations promote transient effects, which can induce both performance benefits and costs (Krebs, Boehler, & Woldorff, 2010; Novak & Foti, 2015; Zhang, Li, Wang, Liu, & Zheng, 2017), while block or group manipulations emphasise sustained attentional costs (Locke & Braver, 2008; Umemoto & Holroyd, 2015). Finally, the studies listed above differed in regards to the relevant trial events: valence was linked either to cues presented prior to the occurrence of the Go/NoGo stimulus (Guitart-Masip et al., 2011; Guitart-Masip et al., 2012; Richter et al., 2014; Schevernels et al., 2016) or linked to the Go/NoGo stimulus itself (Boehler et al., 2012; Freeman, Razhas, & Aron, 2014), thereby tapping into proactive and reactive control mechanisms respectively (Krebs & Woldorff, 2017). The dissociation between cue- and target-based manipulations is highlighted by differential neural patterns found in response to sustained and transient reward manipulations (Beck, Locke, Savine, Jimura, & Braver, 2010; Engelmann, Damaraju, Padmala, & Pessoa, 2009).

In support of approach/avoidance explanations, it has been shown during Go/NoGo tasks that positive incentives speed Go responses, but worsen the stopping rate to NoGo cues, whereas negative incentives improve the rate of stopping to NoGo cues, but slow Go responses (Guitart-Masip et al., 2014; Schutzwohl, 2018). However, such effects could also relate to the attention given to the task under positive and negative incentives. As a successful response to NoGo cues requires no action, improved stopping rates may simply reflect a lack of engagement with the task, giving participants more time to successfully inhibit their response. In support of approach/avoidance interpretations, positive affective states have been shown to

increase attention, while also decreasing subjective effort, while negative affective states have been shown to reduce attention to a task, while also increasing subjective effort (Cabanac, 1971; Fredrickson, Mancuso, Branigan, & Tugade, 2000; Leknes & Tracey, 2008; van Steenbergen, Band, & Hommel, 2009, 2012).

Further, losses may reduce on-task-attention due to their increased emotional salience (Buzzell, Beatty, Paquette, Roberts, & McDonald, 2017; Hartmann et al., 2013; Pratto & John, 1991). In classical theories of attention, an inverted U-shaped association is assumed between attention and task performance (Posner, 1980), where attention is first only paid to task-relevant stimuli, then to irrelevant stimuli as attention increases (Bahrick, Fitts, & Rankin, 1952; Easterbrook, 1959). The asymmetry between losses and gains on attention has been hypothesised to partly explain the divergent effects of losses and gains on motivation and performance, as losses may distract participants from the primary task goals (Yechiam, Retzer, Telpaz, & Hochman, 2015).

Psychological theories stress that decision-making depends on an individual's cognitive frames of the decision-outcomes (Birnberg, Luft, & Shields, 2006). A key finding in this area is that framing an outcome as a loss elicits greater perceived effort and leads to a deterioration in effortful performance when compared to an identical outcome framed as a bonus or a gain (Brooks, Stremitzer, & Tontrup, 2017; Church, Libby, & Zhang, 2008; Gose & Sadrieh, 2012; Hannan, Hoffman, & Moser, 2005; Van de Weghe & Bruggeman, 2006), as well as reducing trust in the experimenter and inducing feelings of unfairness (Christ, Sedatole, & Towry, 2012). Developing on framing research, perceived unfairness has been found to result in reduced effortful performance (Akerlof & Yellen, 1990; Blau, 1993; Byrne, Stoner, Thompson, & Hochwarter, 2005; Hannan et al., 2005; Lindquist, 2010), possibly explaining the

effect of cognitive frames on cognitive effort; they reduce performance through an increase in perceived unfairness.

An alternative explanation for the divergent effect of gains and losses on effortful performance is that it relates to the transmission of dopamine in the prefrontal cortex and striatum (Cools & D'Esposito, 2011). High dopamine in the prefrontal cortex is associated with increased cognitive stability, whereas high dopamine in the VS is associated with increased cognitive flexibility (Aarts, Nusselein, et al., 2014; Hazy, Frank, & O'Reilly, 2006). Cognitive stability is the increased ability to focus and engage cognitive resources to a specific task, whereas cognitive flexibility is associated with an increased ability to seek new information and search for new, more rewarding tasks (Aarts, Wallace, et al., 2014; Cools, Nakamura, & Daw, 2011). However, dopamine can become 'overdosed' in the prefrontal cortex, leading to a deterioration in cognitive stability, with differing optimal dopamine levels found between individuals (Hazy et al., 2006). It has, therefore, been theorised that losses can cause a relative deterioration in performance due to them 'overdosing' dopaminergic levels in the prefrontal cortex, or increasing dopamine levels in the VS, leading to a relative decrease in cognitive stability, and a relative increase in cognitive flexibility (Cools et al., 2011).

Overall, while losses are more motivating than gains of equal nominal value, they do not cause a relative increase in, or may even cause a relative deterioration in, effortful performance. However, the underlying cause behind this divergent effect remains unclear, although it may relate to approach/avoidance associations with gains and losses, dopaminergic innervations in the prefrontal cortex, cognitive frames, or as a combination of the three.

Cognitive effort is conceptualised as a discounting factor in the present thesis, deployed proportional to the SV of associated incentives. It is therefore important to consider the neuroeconomic basis of reward discounting, and to compare effort-based discounting to other discounting factors such as probability and delay to determine whether the present results show any generalisability to these discounting factors

1.4 Cortical Oscillatory Changes

The preceding sections have highlighted the opposing effects of incentive valence and approach/avoidance tendencies on performance in effortful tasks. Amplitude changes in cortical oscillations have previously been associated with varying states of activation and inhibition in many stages of tasks involving cognitive effort, and may therefore prove a useful tool in the investigation of the effect of incentive on effortful engagement.

Instantaneous, fluctuating states of cortical activation and inhibition have previously been investigated using the electrophysiological measure of ERD and ERS (Cassim et al., 2000; Neuper, Wortz, & Pfurtscheller, 2006; Pfurtscheller & Aranibar, 1979; Pfurtscheller, Stancak, & Neuper, 1996). Since the experimental sections of the present thesis rests on the measures of ERD and ERS, the basic neurophysiological features of the phenomenon are outlined in the following sections.

1.4.1 Oscillatory changes associated with motor preparation and control

Unilateral limb movements, real or imagined, are commonly preceded by an ERD and followed by an ERS over sensorimotor areas in both the alpha and beta frequency bands (Chatrian et al., 1959; Cuevas, Cannon, Yoo, & Fox, 2014; Fox et al., 2016; Gastaut, 1952; Leocani, Toro, Manganotti, Zhuang, & Hallett, 1997; Neuper et al., 2006; Pfurtscheller & Aranibar, 1979; Pfurtscheller & Berghold, 1989;

Pfurtscheller & Lopes da Silva, 1999; Salmelin & Hari, 1994; Toro et al., 1994). Historical studies first identified rhythmic alpha- and beta-band suppressions occurring scalp regions from approximately 2 seconds prior to a pre-prepared movement (Chatrian et al., 1959; Gastaut, 1952), with more bilateral patterns of ERD found at the time of movement execution (Alegre et al., 2006; Cassim et al., 2000; Crone et al., 1998; Erbil & Ungan, 2007; Kilavik et al., 2012; Pfurtscheller, Stancak, & Edlinger, 1997; Stancak & Pfurtscheller, 1996; Tzagarakis, Ince, Leuthold, & Pellizzer, 2010). A rebound or synchronisation occurs around 1 second following movement cessation (Salmelin & Hari, 1994). The desynchronization found prior to movement initiation usually occurs over somatosensory areas of the scalp, and is often observed over more posterior areas in the alpha compared to the beta band (Babiloni et al., 2002; Jasper & Penfield, 1949; Jurkiewicz, Gaetz, Bostan, & Cheyne, 2006).

Later studies using ERD analyses (Pfurtscheller and Aranibar, 1977; Pfurtscheller and Lopes da Silva, 1999) quantified these changes in terms of percentage differences in oscillatory power relative to a baseline period. Source localisation methods have further been used to locate the neural generators of alpha- and beta-band oscillatory changes associated with movement preparation and inhibition, finding activation occurring within somatosensory and motor cortices (Brovelli et al., 2004; Klostermann et al., 2007).

ERD in the alpha band is usually viewed as an electrophysiological correlate of cortical activation, showing that a specific region is prepared to process incoming information with increased neuronal excitability (Lopes da Silva, 1991; Neuper et al., 2006; Pfurtscheller & Lopes da Silva, 1999). Pre-movement ERD may reflect motor readiness, or the preparing of sensory and motor neural networks (Foxe & Snyder, 2011; Haegens, Nácher, Luna, Romo, & Jensen, 2011; Klimesch, Sauseng, &

Hanslmayr, 2007; Neuper & Pfurtscheller, 2001a; Neuper et al., 2006). However, no direct connection between alpha-band ERD and muscle activation has been found (Stancak, Riml, & Pfurtscheller, 1997), and while external load has been found to affect the onset and duration of pre-movement alpha-band ERD, it has not been found to affect its magnitude (Leocani, Toro, Zhuang, Gerloff, & Hallett, 2001). It has, therefore, been argued that pre-movement alpha-band ERD may be indicative of regions which guide movement, but which are not required for the movement itself (Crone et al., 1998).

Amplitude attenuation of cortical oscillations in the beta band (16-24 Hz) relating to motor preparation over sensorimotor regions of the scalp have been investigated since early studies on electrophysiological responses to stimuli (Berger, 1929; Jasper & Penfield, 1949). Early research found a similar pre-movement effect to the alpha-band, with an ERD over contralateral sensorimotor areas preceding voluntary movements (Babiloni et al., 2002; Jasper & Penfield, 1949; Jurkiewicz, Gaetz, Bostan, & Cheyne, 2006; Keinrath, Wriessnegger, Muller-Putz, & Pfurtscheller, 2006; Koelewijn, van Schie, Bekkering, Oostenveld, & Jensen, 2008; McFarland, Miner, Vaughan, & Wolpaw, 2000; Nakagawa et al., 2011; Pfurtscheller, Graimann, Huggins, Levine, & Schuh, 2003; Salmelin & Hari, 1994), becoming bilateral during movement execution (Alegre et al., 2006; Cassim et al., 2000; Crone et al., 1998; Doyle, Yarrow, & Brown, 2005; Erbil & Ungan, 2007; Kilavik et al., 2012; Omlor, Patino, Mendez-Balbuena, Schulte-Monting, & Kristeva, 2011; Pfurtscheller, Stancak, & Edlinger, 1997; Stancak & Pfurtscheller, 1996; Tzagarakis, Ince, Leuthold, & Pellizzer, 2010; Wheaton, Fridman, Bohlhalter, Vorbach, & Hallett, 2009), and followed by ERS seconds after movement cessation (Baker, Kilner, Pinches, & Lemon, 1999; Jurkiewicz et al., 2006; Pfurtscheller, Stancak, & Neuper,

1996; Spinks, Kraskov, Brochier, Umilta, & Lemon, 2008; van Elk, van Schie, van den Heuvel, & Bekkering, 2010).

However, while the pre-movement ERD in the alpha band is considered to reflect motor control or sensory integration, in the beta-band it is considered to be the undifferentiated reflection of motor preparation (Erbil & Ungan, 2007; Pfurtscheller, Stancak, et al., 1996; Stancak & Pfurtscheller, 1996). Pre-movement beta-band ERD has been localised to several motor-related brain networks (Brovelli et al., 2004; Klostermann et al., 2007) and is most prominent in peri-Rolandic regions (Murthy & Fetz, 1996; Pfurtscheller & Berghold, 1989; Pfurtscheller & Neuper, 1997; Schnitzler, Salenius, Salmelin, Jousmaki, & Hari, 1997). It is also associated with an increase in corticospinal excitability (Chen, Yaseen, Cohen, & Hallett, 1998; Rau, Plewnia, Hummel, & Gerloff, 2003), as well as an increase in the BOLD signal in the motor cortex (Formaggio et al., 2008; Stevenson, Brookes, & Morris, 2011; Yuan et al., 2010).

Several studies have investigated modulations in sensorimotor alpha- and beta-band ERD during movement preparation (Yamanaka & Yamamoto, 2010; Leocani, Toro, Zhuang, Gerloff, & Hallett, 2001; Filipović, Jahanshahi, & Rothwell, 2001; Alegre et al., 2004; Harmony, Alba, Marroquín, & González-Frankenberger, 2009). This research has generally found stronger sensorimotor beta-band ERD during the initiation of Go responses compared to their inhibition in NoGo trials **(**Filipović, Jahanshahi, & Rothwell, 2001; Alegre et al., 2004), but no significant differences in the alpha band (Alegre et al., 2004; Iijima et al., 2015; Filipović, Jahanshahi, & Rothwell, 2001). Expanding on this research, Liebrand, Pein, Tzvi, and Krämer (2017) investigated the effect of approach/avoidance motor-sets on proactive control using ERD measures during a pre-cued Go/NoGo task. Trials where participants expected a

Go cue with a 100% probability of occurrence were compared to trials with equiprobable subsequent Go/NoGo cues. Liebrand, Pein, Tzvi, and Krämer (2017) found significantly stronger beta-band ERD over ipsilateral sensorimotor areas and weaker alpha-band ERD over posterior-parietal areas in trials with a certain subsequent Go cue. It therefore appears that sensorimotor beta-band ERD is reflective of the strength of approach motor-sets, while posterior-parietal alpha-band ERD is reflective of response certainty or anticipation.

However, sensorimotor beta ERD is not affected by several different movement parameters, including; the speed, rate, and velocity of responses (Cassim et al., 2000; Fry et al., 2016; Stancak & Pfurtscheller, 1995; Stancak & Pfurtscheller, 1996; Tombini et al., 2009); the number of fingers involved in a movement (Salmelin et al., 1995); whether the movement is ballistic or sustained (Alegre et al., 2003); contraction force (Cremoux, Tallet, Berton, Dal Maso, & Amarantini, 2013; Stancak et al., 1997); movement length and target direction (Tatti et al., 2019) or the weight of a manipulated load (Pistohl, Schulze-Bonhage, Aertsen, Mehring, & Ball, 2012; Stancak et al., 1997). Beta ERD is also found in settings where no movement is made, such as motor planning (Liddle et al., 2016; Tzagarakis et al., 2010; van Wijk, Beek, & Daffertshofer, 2012) and imagery (Pfurtscheller, Neuper, Brunner, & da Silva, 2005; Schnitzler et al., 1997).

Beta ERD has therefore been suggested to reflect the execution or selection of internally generated motor models (Kilner, Friston, & Frith, 2007; Miall, 2003; Palmer, Zapparoli, & Kilner, 2016). The idea that beta-band ERD reflects the execution or selection of internally generated motor models is supported by the observation that the uncertainty of an action's direction can decrease the magnitude of the pre-movement ERD (Kaiser, Birbaumer, & Lutzenberger, 2001; Tzagarakis et al.,

2010; Tzagarakis, West, & Pellizzer, 2015) and that the onset of beta ERD varies with the strength of motor preparation (Alegre et al., 2003; Kaiser et al., 2001; Kilner, Bott, & Posada, 2005) and with faster RTs (Doyle et al., 2005; Williams et al., 2003).

The bilateral pattern of beta-band ERD occurring during movement execution has also been shown to occur preceding movements with a higher rate of force (Hortobagyi, Taylor, Petersen, Russell, & Gandevia, 2003; Perez & Cohen, 2008; Stedman, Davey, & Ellaway, 1998; Stinear, Walker, & Byblow, 2001; Tinazzi & Zanette, 1998). Ipsilateral beta-band ERD has been proposed to represent a process of interhemispheric inhibition, by which activation in the ipsilateral cortex is prevented from interfering with the unilateral movement (Fujiyama, Hinder, & Summers, 2013; Welniarz, Dusart, Gallea, & Roze, 2015). The view that ipsilateral beta-band ERD represents interhemispheric inhibition was developed following the observations that trans-colossal homologous movements have been found to require inhibition during the generation of unilateral movements (Erbil & Ungan, 2007) and that damage to the corpus callosum has been found to cause mirror movements (Rothwell et al., 1991).

The patterns of pre-movement ERD and ERS in the alpha and beta bands associated with movement show many similarities. However, oscillatory changes in the alpha band likely reflect the inhibition and activation of sensorimotor integration or guiding of motor activity, while changes in the beta band may show the maintenance and release of internally generated motor sets.

1.4.2 ERS and cortical inhibition

ERS in the alpha and beta bands is commonly thought to reflect cortical idling (Pfurtscheller, Stancak et al., 1996) or inhibition (Cassim et al., 2001; Cassim et al., 2000; Gaetz, Edgar, Wang, & Roberts, 2011), as well as sensory reafference (Cassim et al., 2001). Brain regions which are activated during a task exhibit alpha- and beta-

band ERD, while brain regions which are inhibited exhibit ERS (Foxe & Snyder, 2011; Fu et al., 2001; Jokisch & Jensen, 2007; Kelly, Lalor, Reilly, & Foxe, 2006; Rihs, Michel, & Thut, 2007; Worden, Foxe, Wang, & Simpson, 2000; Yamagishi et al., 2003). Alpha-band activity has also been found to respond to modality specific changes. For example, alpha power increases selectively over parietal-occipital regions when participants are cued to attend to an auditory feature of a multi-sensory stimulus, indicating the suppression of visual processing (Foxe & Snyder, 2011; Fu et al., 2001; Snyder & Foxe, 2010).

Post-movement beta ERS is highly sensitive to task parameters, being larger with a heavy resistance load (Stancak et al., 1997), fatigue (Fry, Mullinger, O'Neill, Brookes, & Folland, 2017) and the force and rate of movements (Fry et al., 2016). The post-movement ERS has been hypothesised as representing the interplay between sensory and motor regions related to long-range integrative processes (Cassim et al., 2000; Shimazu et al., 1999; Tewarie et al., 2018), being representative of top-down inhibitory control (Solis-Escalante, Muller-Putz, Pfurtscheller, & Neuper, 2012; Tewarie et al., 2018). Supporting this hypothesis are the observations that a treatment with benzodiazepines increases the resting level of beta oscillations in the sensorimotor cortex (Jensen & Lisman, 2005) and that GABA levels in the motor cortex correlate with rebound magnitude (Gaetz & Cheyne, 2006).

Beta oscillations have also been shown to increase in power during episodes of static postural maintenance (Baker, Olivier, & Lemon, 1997; Conway et al., 1995; Donoghue, Sanes, Hatsopoulos, & Gaal, 1998; MacKay & Mendonca, 1995; Rougeul, Bouyer, Dedet, & Debray, 1979; Sanes & Donoghue, 1993; Spinks et al., 2008; van Elk et al., 2010). In this research, simple ‘hook’ grips cause a larger increase in beta power relative to a more complex ‘precision’ grip involving the thumb (Spinks et al.,

2008), and larger power is found for meaningless compared to meaningful hand postures (van Elk et al., 2010). Beta oscillations also show significant coherence and phase synchrony with the EMG recordings of muscle activations (Feige, Aertsen, & Kristeva-Feige, 2000; Witham, Riddle, Baker, & Baker, 2011). Steady muscle contractions are maintained by a continuous drive from the motor cortex to spinal motor neurons (Scott, 2012), during which there is a relative increase in beta power compared to dynamic contractions (Baker et al., 1997; Cassim et al., 2000; Espenhahn, de Berker, van Wijk, Rossiter, & Ward, 2017; Kilner et al., 1999; Kilner et al., 2003; Schoffelen, Oostenveld, & Fries, 2008; Spinks et al., 2008; van Wijk et al., 2012).

The investigation of beta oscillations during static postural maintenance led sensorimotor beta ERS to be considered as reflecting the active maintenance of existing cognitive motor sets, in line with the view that ERD represents the execution or release of motor sets (Androulidakis, Doyle, Gilbertson, & Brown, 2006; Androulidakis et al., 2007; Baker, 2007; Engel & Fries, 2010; Gilbertson et al., 2005; Pogosyan, Gaynor, Eusebio, & Brown, 2009)

Further, a strong association has been found between beta-band ERS over right frontal areas and motor inhibition, in line with the view that motor inhibition is implemented by the inferior frontal cortex (Buschman & Miller, 2007, 2009; Siegel, Donner, Oostenveld, Fries, & Engel, 2008). Beta-band power has also been shown to be higher in right frontal regions and the basal ganglia preceding successful compared to failed stop trials during stop-signal tasks (Fonken et al., 2016; Ray et al., 2012; Swann et al., 2009; Wagner, Wessel, Ghahremani, & Aron, 2018; Wessel & Aron, 2013; Zavala et al., 2018). Similarly, a quantifiable relationship between beta power amplitude and local concentrations of GABA (Gaetz et al., 2011; Hall, Barnes, Furlong, Seri, & Hillebrand, 2010; Hall et al., 2011; Jensen & Lisman, 2005;

Muthukumaraswamy et al., 2013; Roopun et al., 2006; Rossiter, Davis, Clark, Boudrias, & Ward, 2014), as well as decreases in cortical excitability (Hsu et al., 2011; McAllister et al., 2013; Noh, Fuggetta, Manganotti, & Fiaschi, 2012) has been found.

Typically occurring in the absence of sensory processing or motor action, sensorimotor alpha-band rhythms were initially considered to reflect idling of the sensorimotor cortex (Mulholland, 1995; Pfurtscheller, Stancak, & Neuper, 1996). The hypothesis that alpha band rhythms reflect cortical idling was bolstered by the observation of focal ERD and surround ERS (Suffczynski, 1999), which was interpreted as a type of lateral cortical idling of regions not involved in motor preparation (Neuper et al., 2006). However, more recent conceptualisations have considered alpha-band ERS as reflecting active inhibition to prevent inappropriate muscle activation on movement cessation (Foxe & Snyder, 2011; Haegens, Nácher, et al., 2011; Hummel & Gerloff, 2005; Klimesch et al., 2007; Pineda, 2005). The link between the alpha rhythm and physiological inhibition was established in the 1960s, by employing GABAergic agonists, when robust spindling activity with a very similar frequency as resting alpha was found, leading to the creation the alpha-pacemaker hypothesis (Andersen & Andersson, 1968). Years later, it was demonstrated that the proposed spindle activity induced by GABAergic agonists and the classical alpha rhythm were dissociable phenomena (Lopes da Silva, Vos, Mooibroek, & Van Rotterdam, 1980). These findings relaxed the alpha pacemaker hypothesis, establishing the thalamus as a prominent alpha source (Lopes da Silva et al., 1980), in addition to its occipital sources (Lopes da Silva et al., 1980).

Theoretical frameworks assign alpha oscillations a functional inhibitory role (Foxe & Snyder, 2011; Jensen, Bonnefond, & VanRullen, 2012; Jensen & Mazaheri, 2010; Klimesch, 2012b; Klimesch et al., 2007; Mathewson et al., 2011; Mazaheri &

Jensen, 2010; Weisz, Hartmann, Müller, Lorenz, & Obleser, 2011), implemented through physiological inhibition (Jensen et al., 2012; Jensen & Mazaheri, 2010; Klimesch et al., 2007; Mazaheri & Jensen, 2010). Functional inhibition could be a consequence of physiological 'pulsed' inhibition produced by GABAergic feedback carried by inter-neurons within the cortex or thalamus (Gips, van der Eerden, & Jensen, 2016; Jensen et al., 2012; Jensen & Mazaheri, 2010; Mazaheri & Jensen, 2010). Other recent frameworks, although highlighting the inhibitory role of alpha, widen the physiological hypothesis stressing the importance of the excitatory and inhibitory balance to control alpha amplitude and frequency (Himmelstoss et al., 2015; Klimesch, 2012b).

The inhibition-timing hypothesis (Klimesch et al., 2007) states that alpha activity reflects a top-down inhibitive process, where there is a timed build-up and release of information controlled by alpha-band activity. It has been hypothesised that task-relevant increases in alpha power may relate to the timing of inhibition rather than the inhibition itself (Benedek, Bergner, Konen, Fink, & Neubauer, 2011; Jauk, Benedek, & Neubauer, 2012; Klimesch, 2012b).

While it has been hypothesised that alpha-band activity represents the pulsed inhibition of neural regions through GABAergic neuron firing (Jensen & Mazaheri, 2010), the application of Benzodiazepines (a GABA agonist) often does not lead to increased alpha activity but instead a decrease in occipital alpha-band power during resting state (Ahveninen et al., 2007; Alonso et al., 2015; Berchou, Chayasirisobhon, Green, & Mason, 1986; Boeijinga et al., 2004; Connemann et al., 2005; Feshchenko, Veselis, & Reinsel, 1997; Fingelkurts et al., 2004; Fink, Weinfeld, Schwartz, & Conney, 1976; Golombok & Lader, 1984; Liley, Cadusch, Gray, & Nathan, 2003; Link, Leigh, & Fell, 1991; Lozano-Soldevilla, ter Huurne, Cools, & Jensen, 2014;

Schreckenberger et al., 2004; Van Steveninck et al., 1993; Yoto et al., 2012). In contrast, reports of Benzodiazepines increasing posterior alpha power (Nikulin, Nikulina, Yamashita, Rossi, & Kähkönen, 2005; Tran, Craig, Bartrop, & Nicholson, 2004), or causing non-significant differences (Muthukumaraswamy et al., 2013; Urata et al., 1996) are much less common.

One possible explanation for the decrease of alpha power with GABA innervations is that classical alpha oscillations rely on the balance between physiological excitation and inhibition (Anderson, Carandini, & Ferster, 2000; Himmelstoss et al., 2015; Okun & Lampl, 2008). Supporting the role of the balance between physiological excitation and inhibition on alpha rhythms is the observation that the firing rate of pyramidal cells is reduced during pharmacological inhibition, causing a decrease in alpha power (Jones et al 2000). Recent computational models have also highlighted the interplay between inhibition and excitation in the alpha rhythm (Jones & Rachlin, 2009).

Increases in cortical oscillatory power in the alpha band is commonly associated with the active inhibition of specific cortical regions, with a possible role of activity in the alpha frequency range being to control the timing of cortical responses. In contrast, an increase in power in the beta band, especially over right frontal regions of the scalp, is more specifically related to the inhibition of prepared motor actions.

1.4.3 Alpha-band ERD during anticipatory attention.

Attention provides a mechanism that allows the enhancing of relevant information and the suppression of irrelevant information (Kastner & Ungerleider, 2000). To attain this, attention results in competitive interactions among neurons,

causing to them to respond more strongly to attended stimuli while distracting stimuli are suppressed (Desimone & Duncan, 1995).

Alpha ERD across the whole scalp is associated with attentional processing (Carp & Compton, 2009; Foxe & Snyder, 2011; Jensen & Hanslmayr, 2020; Klimesch, 1999; Klimesch, 2012b; Rohenkohl & Nobre, 2011; Tang, Hu, & Chen, 2013; Wu et al., 2015), commonly occurring during mental arithmetic (Creutzfeldt, Grünewald, Simonova, & Schmitz, 1969), and attentional tasks (Boiten, Sergeant, & Geuze, 1992; Krause, Lang, Laine, Kuusisto, & Porn, 1995; Sergeant, Geuze, & Van Winsum, 1987; Sterman, Kaiser, & Veigel, 1996; Van Winsum, Sergeant, & Geuze, 1984). Oscillations in the alpha band are associated with the distribution of attention through the strategic activation and inhibition of neural regions, with ERD being found over task-relevant areas and ERS over task-irrelevant areas (Anderson & Ding, 2011; Bauer, Kennett, & Driver, 2012; Bauer, Oostenveld, Peeters, & Fries, 2006; Bonnefond & Jensen, 2012; Busch & VanRullen, 2010; Foxe & Snyder, 2011; Frey et al., 2014; Haegens, Händel, & Jensen, 2011; Handel, Haarmeier, & Jensen, 2011; Jensen et al., 2012; Jensen & Mazaheri, 2010; Kelly et al., 2006; Klimesch, 1999; Klimesch, 2012a; Rihs et al., 2007; Romei, Gross, & Thut, 2010; van Ede, de Lange, Jensen, & Maris, 2011; Worden et al., 2000).

Visual attention has been shown to be intrinsically related to modulations in alpha-band oscillations (Bastiaansen, Böcker, & Brunia, 2002; Bastiaansen, Bocker, Brunia, de Munck, & Spekreijse, 2001; Capotosto, Babiloni, Romani, & Corbetta, 2009; Donner et al., 2007; Foxe & Snyder, 2011; Handel et al., 2011; McDermott, Wiesman, Proskovec, Heinrichs-Graham, & Wilson, 2017; Onoda et al., 2007; Proskovec, Heinrichs-Graham, Wiesman, McDermott, & Wilson, 2018; Siegel, Donner, Oostenveld, Fries, & Engel, 2007; Vanni, Revonsuo, & Hari, 1997; Wiesman,

Heinrichs-Graham, Proskovec, McDermott, & Wilson, 2017; Yamagishi, Goda, Callan, Anderson, & Kawato, 2005). Parieto-occipital ERD is closely related to anticipatory attention (Bonnefond & Jensen, 2012; Jensen & Mazaheri, 2010; Rihs et al., 2007; Spaak, de Lange, & Jensen, 2014; van Dijk, Schoffelen, Oostenveld, & Jensen, 2008), particularly prior to the onset of a salient visual stimulus or during the maintenance phase of visual working memory tasks (Bonnefond & Jensen, 2012; van Dijk, Nieuwenhuis, & Jensen, 2010; Wilson et al., 2017). Amplitude modulations in the alpha band have been used to predict, trial by trial, the speed of visual perception (Thut, Nietzel, Brandt, & Pascual-Leone, 2006) and mirror BOLD changes found in the FPN during visual attention (Sestieri et al., 2008; Sylvester, Jack, Corbetta, & Shulman, 2008; Sylvester, Shulman, Jack, & Corbetta, 2007).

It has been hypothesised that the FPN controls anticipatory attention in occipital and parietal occipital regions by maintaining visual expectations through the desynchronization of ongoing alpha rhythms (Capotosto et al., 2009; Corbetta & Shulman, 2002; Coull, Walsh, Frith, & Nobre, 2003; Kastner & Ungerleider, 2000; Serences & Yantis, 2006). The hypothesis of FPN control is supported by TMS studies reporting deficits in visual stimulus processing after interference with TMS over posterior parietal and frontal parietal regions (Capotosto et al., 2009; Chambers, Payne, Stokes, & Mattingley, 2004; Grosbras & Paus, 2002, 2003; Heinrichs-Graham, McDermott, Mills, Coolidge, & Wilson, 2017; Herring, Thut, Jensen, & Bergmann, 2015; Hilgetag, Théoret, & Pascual-Leone, 2001; Pascual-Marqui, Michel, & Lehmann, 1994; Romei et al., 2010; Thut, Nietzel, & Pascual-Leone, 2005; Wilson, McDermott, Mills, Coolidge, & Heinrichs-Graham, 2018). For example, Capotosto et al. (2009) used repetitive TMS to systematically disrupt alpha oscillations in the right parietal and frontal cortices prior to the performance of a visual target identification

task. They showed that this disruption of impaired participants' ability to identify subsequently presented targets in the visual space, and that this covaried significantly with the level of alpha disruption in parietal and occipital electrodes.

Attentional processes are commonly reflected in changes in cortical oscillatory power in the alpha band, especially anticipatory attention controlled by the FPN. Cortical rhythms in the alpha frequency range may control the strategic activation and inhibition required for sustained attention rather than directly reflecting cognitive effort or control processes.

1.4.4 Cognitive effort and control reflected in theta-band synchronisation

While oscillatory activity in the alpha band is generally associated with visual attention or the inhibitive processes associated with attentional orienting, activity in the theta frequency-range over midline frontal areas is generally found to increase in power when higher levels of mental effort are required (Amin, Malik, Hussain, Kamel, & Chooi, 2014; Cavanagh & Frank, 2014; Inanaga, 1998; Jensen & Tesche, 2002; Lin, Jung, Wu, Lin, & She, 2012; Lundqvist, Herman, & Lansner, 2011). Oscillatory activity in the theta band appears to reflect the active maintenance of high-level cognitive processes such as working memory, novelty detection, and cognitive control (Cavanagh, Zambrano-Vazquez, & Allen, 2012; Itthipuripat, Wessel, & Aron, 2013; Jacobs, Hwang, Curran, & Kahana, 2006; Rutishauser, Ross, Mamelak, & Schuman, 2010), and has been considered to be a potential indicator of cognitive effort or control (Itthipuripat et al., 2013).

Sustained enhancements of theta-band power over midline frontal areas have repeatedly been observed during difficult listening tasks (Kolev, Yordanova, Schürmann, & Baţar, 1999; Mazaheri & Picton, 2005; McMahon et al., 2016; Obleser,

Wöstmann, Hellbernd, Wilsch, & Maess, 2012; Pesonen, Björnberg, Hämäläinen, & Krause, 2006; Wisniewski, 2017; Wisniewski et al., 2015). For example, frontal-midline theta power increases have been found as the signal to noise ratio decreases during sentence recognition (Wisniewski et al., 2015). The same is not observed while listeners hear speech in noise while watching silent movies (Dimitrijevic, Smith, Kadis, & Moore, 2017; Wisniewski et al., 2015).

Further, theta dynamics have repeatedly been associated with broader working memory and cognitive control processes. Frontal midline enhancements are well known to vary as a function of working memory load in nonauditory paradigms (Gevins, Smith, McEvoy, & Yu, 1997; Jensen & Tesche, 2002; Klimesch, Schack, & Sauseng, 2005; Onton, Delorme, & Makeig, 2005), and have been hypothesised to reflect the increased utilization of working memory resources during effortful listening (Rönnberg et al., 2013; Rönnberg, Rudner, Foo, & Lunner, 2008). Theta-band synchronisation is further associated with extended periods of effortful engagement (Asada, Fukuda, Tsunoda, Yamaguchi, & Tonoike, 1999; Barwick, Arnett, & Slobounov, 2012; Hsieh & Ranganath, 2014; Ishii et al., 1999; Mitchell, McNaughton, Flanagan, & Kirk, 2008; Paus et al., 1997; Wascher et al., 2014), suggesting theta-band activation contributes to sustaining effortful behaviour in the face of growing mental fatigue rather than phasic increases in cognitive effort in response to incentive or task cues (Umemoto, Inzlicht, & Holroyd, 2019).

Overall, increases in power in the theta frequency range over frontal-midline areas of the scalp are often found to correlate with task difficulty, and especially with listening effort and working memory load. Theta-band synchronisation over frontal midline areas is hypothesised to reflect sustained effortful engagement rather than phasic increases in cognitive control.

Chapter 2 – General methods

2.1 Cognitive Effort Tasks

There are several methods which can be used to investigate the interaction between reward and cognitive effort. An early method used to measure phenomenological effort was through the use of self-reports (Efklides, Kourkoulou, Mitsiou, & Ziliaskopoulou, 2006; Meyer & Hallermann, 1977; Roets, Van Hiel, Cornelis, & Soetens, 2008). However, self-report measures may not be an effective measure of effortful engagement as they are highly vulnerable to self-presentational influences (Efklides et al., 2006; Meyer & Hallermann, 1977; Roets et al., 2008) and because participants may not accurately report their efforts due to limited introspection abilities (Wilson, 2004).

Another way to investigate effort-based decision-making is through the choice to engage in effortful outcomes during a discounting task. Discounting tasks do not measure cognitive effort directly but allow researchers to quantify in monetary terms the discounting effect of effortful requirements, thus providing a formalized neuroeconomic conception of the SV of effort as a discounting factor. Individual discounting rates may be related to how cognitive resources are deployed during effortful tasks, however a direct relationship between discounting rates and cognitive effort is yet to be established. Conversely, how incentives alter effortful performance could be investigated. Rather than investigating how effort discounts reward, an incentive-based approach can be used to show how reward alters performance measures associated with effort and the processes associated with such. Measures of effortful performance (e.g., RTs, items remembered from a list, mathematical speed or accuracy) are commonly used to make inferences about the amount of effort invested into a task under different conditions (Bandura, 1991; Bijleveld, Custers, & Aarts,

2010; Eisenberger, 1992; Kukla, 1972; Locke & Latham, 1990). For example, it could be investigated how incentive modulates RTs during MID, or sustained vigilance tasks. However, effortful performance may be affected by factors other than effort alone (e.g., ability, practice, and strategy) (Locke & Latham, 1990), and may not be appropriate as a direct measure of the effort invested during a task.

The research discussed in the present thesis used RTs and NoGo stopping rates as measures of effortful performance, investigated when participants were offered incentives of differing valences/magnitudes. ERD/ERS measures were used in concert with measures of effortful behaviour to investigate the cortical underpinnings of how incentive modulates effortful performance.

Finally, effort can be investigated using physiological or neural responses associated with the deployment of effortful resources. For example, CV responses, especially the cardiac pre-ejection period, have been used to infer effortful engagement (Berntson, Lozano, Chen, & Cacioppo, 2004; Elliott, 1969; Obrist, 1976), and a combination of EEG, pupillometric response, and skin conduction has been used as measures of task engagement (Csibra & Johnson, 2013). Similarly, changes in cortical oscillatory power associated with cortical activation and inhibition could be used concurrent to behavioural measures of effortful performance and SV.

2.1.1 Discounting task

SV is often used to provide a direct measure of the discounting effects of cognitive effort and other factors on the valuation of monetary rewards. The COGED paradigm can be used to estimate the SV of differing effort levels in terms of their discounting effect on associated rewards (Massar, Lim, Sasmita, & Chee, 2016; Westbrook & Braver, 2015).

In the COGED paradigm, participants are familiarized with several levels of a cognitively demanding task. Following the familiarization stage, participants are offered a series of choices presented in pairs. One option in the presented choice consists of a high-effort version of the familiarized task, and the other a low-effort version, with more money offered for the higher-effort option. Multiple choices are made, and the amounts offered for the low-effort option are step-wise iterated (increased if the participant chooses the high-effort option and decreased if they choose the low-effort option) until an indifference point can be established between the two options.

The pattern of indifference points calculated in this task can be used to quantify differences in effort discounting across multiple levels of the task and show individual discounting rates in quantifiable monetary terms rather than simply showing the direction of the discounting effect (Massar et al., 2016; Westbrook & Braver, 2015). Individual discounting rates are usually assessed by calculating the AuC of the indifference points across multiple effort levels. The benefits of using the AuC as a measure of individual effort-discounting rates is that it allows for the quantification of discounting patterns without fitting the curves to theoretical models requiring normally distributed data (Smith, Lawyer, & Swift, 2018).

The research presented in this thesis used a COGED task as a measure of individual effort discounting rates in gain and loss domains. Individual discounting rates were then correlated with changes in performance and in EEG responses as a result of different reward levels.

2.1.2 Vigilance task

Investigating the SV of effort discounting can enable greater understanding of the valuation processes made during the choice to engage with an effortful task.

However, this may differ from the way different incentives motivate the deployment of effortful resources.

Performance-based rewards have been shown to be effective motivators of effortful behaviour (Wise, 2004), ranging from response-speed (Bijleveld, Custers, & Aarts, 2010; Knutson et al., 2001), visual discrimination (Engelmann & Pessoa, 2007; Kristjansson, Sigurjonsdottir, & Driver, 2010), and cognitive control (Locke & Braver, 2008). The subjective devaluation of reward with required effort in choice tasks has also been dissociated from the effect of reward on effortful behaviour (Bonner, Hastie, Sprinkle, & Young, 2000; Camerer & Hogarth, 1999).

Typical measures of effortful performance in neuropsychological tests include measures of response accuracy or speed (Lezak, Howieson, Loring, & Fischer, 2004). Changes in RT speed and variability have been observed across a variety of tasks designed to assess a range of cognitive skills including response inhibition (Zeeuw et al., 2008; Hervey et al., 2006; Klein, Wendling, Huettner, Ruder, & Peper, 2006; Rubia et al., 2001; Uebel et al., 2010; Vaurio, Simmonds, & Mostofsky, 2009), working memory (Buzy, Medoff, & Schweitzer, 2009; Karatekin, 2004; Klein et al., 2006), attention (Johnson, Häubl, & Keinan, 2007), and simple choice tasks (Andreou et al., 2007).

The motivated vigilance task used in the present thesis is an adaption of the psychomotor vigilance task used by Dinges and Powell (1985). This is a 10-minute sustained attention task, where participants are asked to respond with a button press as quickly as possible upon the appearance of a running millisecond counter. Attentional performance can be quantified by the median RT across trials (Basner & Dinges, 2011), which has been associated with larger pupil dilation with increasing reward

(Massar et al., 2016), indicative of the increased allocation of attentional resources (Kahneman & Beatty, 1966).

2.1.3 Monetary incentive delay task

A similar task is the MID task (Knutson et al., 2000), which requires participants to respond to pre-cued target stimuli with various levels of incentives given. The incentive is indicated by a cue stimulus presented seconds before the target stimulus. Each trial, participants either win or lose small amounts of money based on their RT. While several versions of this task exist, all subdivide events comprising reward anticipation and receipt from events comprising loss anticipation and receipt (Balodis & Potenza, 2015; Patel et al., 2013).

The MID task has been used to study the neurobiological mechanisms of reward processing (Knutson & Greer, 2008; Lammel, Ion, Roeper, & Malenka, 2011; Pignatelli & Bonci, 2015), as well as the effect of effort-based incentives on neural responses (Knutson et al., 2001), both during anticipation and receipt, giving flexibility in the investigation of the effect of reward on effortful implementation.

The cued vigilance tasks and Go/NoGo tasks used in the reported research of the present thesis incorporate elements from the MID task, using cues to inform participants of the value of the current trial seconds before the target stimulus.

2.1.4 Go/NoGo task

Inhibitory control has been investigated using a variety of computerised tasks, including the stop-signal and Go/NoGo tasks (Asci, Braem, Park, Boehler, & Krebs, 2019; Logan & Cowan, 1984; Verbruggen & Logan, 2008; Verbruggen, Stevens, & Chambers, 2014). Go/NoGo and stop-signal tasks place emphasis on successful

inhibition in a context where rapid responding is required most of the time (Logan & Cowan, 1984; Verbruggen & Logan, 2008; Verbruggen et al., 2014).

The Go/NoGo task was created by Donders (1969), and later developed by Bokura, Yamaguchi, and Kobayashi (2001). In this task, participants are required to execute a motor response as quickly as possible whenever they see a Go signal and withhold their response whenever they see a NoGo signal. The similar stop-signal task was created by Logan and Cowan (1984), requiring participants to execute a motor response as quickly as possible whenever presented with a Go signal. A short time after the presentation of the Go signal, a stop signal is presented, requiring participants to withhold their previously prepared response.

While there are strong similarities between the two tasks, both yielding a valid index of inhibitory control (Diamond, 2013), each may capture different aspects of control. For example, in a Go/NoGo task, the requirement to inhibit the prepared response is consistently mapped onto a temporal cue, whereas in stop-signal tasks, the Go cue is always presented before the stop-signal, and the requirement to inhibit is not temporally consistent (Verbruggen & Logan, 2008). It is generally considered that Go/NoGo tasks measure the inhibition necessary for action constraint and stop-signal tasks measure action cancellation (Eagle et al., 2008; Verbruggen & Logan, 2008).

There are several experimental factors that must be considered when designing a Go/NoGo task. For example, a smaller proportion of NoGo trials will make it harder for participants to inhibit inappropriate responses (Menon, Adleman, White, Glover, & Reiss, 2001), as will smaller inter-trial intervals (Garavan, Ross, & Stein, 1999). However, despite these findings, approximately 40% of published studies use equiprobable Go/NoGo stimuli and 20% use trial durations longer than 4 seconds (Wessel & Aron, 2017).

The Go/NoGo task reported in the present thesis was a modification of a cued Go/NoGo task (Filipovic, Jahanshahi, & Rothwell, 2000; Randall & Smith, 2011). Participants were cued of the incentive offered per trial as well as the probability of a subsequent Go or NoGo stimulus. Participants received the incentive if they responded faster than their median RT to a Go cue or successfully withheld their response to a NoGo cue.

2.2 General Principals of EEG

2.2.1 Physiological basis of cortical rhythms

An EEG consists of a series of electrodes which can be used to measure the electrical potentials found along the scalp (Speckmann, Elger, & Gorji, 2011). The history of the measurement of brain oscillations through electroencephalography dates to 1929, with the measure of the spontaneous alpha wave in humans (Berger 1929). Over the ensuing decades, research using these measures continued (Karakaş & Barry, 2017), with cortical oscillations being shown in vitro (Basar, 1976; Başar & Weiss, 1981; Eckhorn et al., 1988; Jahnsen & Llinás, 1984), in the nervous system of vertebrates and invertebrates (Green & Arduini, 1954), as well as in humans(Bernat, Malone, Williams, Patrick, & Iacono, 2007; Besle et al., 2011; Cravo, Rohenkohl, Wyart, & Nobre, 2013; Gomez-Ramirez et al., 2011; Henry & Obleser, 2012; Ishii et al., 2009; Jones & Rachlin, 2006; Kösem, Gramfort, & van Wassenhove, 2014; Stefanics et al., 2010).

Activity found across the scalp is the result of the electrical impulses passed between the billions of neurons that make up the cortex, propagated along the axons (Lent, Azevedo, Andrade-Moraes, & Pinto, 2012). Each neuron produces a small electric potential when it fires, resulting in an equally small local field potential (Herreras, 2016).

EEG recordings are generally thought to be a direct measure of the postsynaptic currents produced by the firing of large clusters of neurons acting in synchrony rather than their action potentials (Nunez & Srinivasan, 2006; Teplan, 2002). While action potentials produce oscillations of a very high frequency, cortical tissue usually filters high-frequency currents, attenuating the oscillations produced by action potentials, whereas the activity produced by postsynaptic potentials act at a much lower frequency and can therefore travel the distance required to reach the scalp (Bedard, Kroger, & Destexhe, 2006).

Electrical signals on the scalp are produced by the partial synchronisation of synaptic activity over macroscopic (cm), regional, and even whole brain spatial sequences (Nunez, 2000; Nunez & Srinivasan, 2006). Although once viewed as a form of 'noise', this synchronisation is now considered to optimize relations between spike-mediated 'top-down' and 'bottom-up' communication within and between brain regions (Fries, Reynolds, Rorie, & Desimone, 2001; Salinas & Sejnowski, 2001; von Stein, Chiang, & Konig, 2000).

Cortical oscillations measured by an EEG can be analysed using three forms of information taken from the waveform: amplitude, phase, and frequency (Klimesch, 2012a). The traditional analysis of EEG data in relation to specific sensory or cognitive events is typically done using one of two approaches. In the time-domain approach, a set of epochs phase-locked to a certain class of events are averaged, producing an ERP at each channel. Alternately, in the frequency-domain, changes in the power spectrum of cortical oscillations are time-locked and averaged to a certain class of events (Makeig, 1993).

2.2.2 Advantages/disadvantages of EEG

The main advantage of EEG over other measures is the high-degree of temporal resolution provided, with the investigation of the dynamics of neural processes on the millisecond level (Luck, 2005; Schneider & Strüder, 2012). Alternative methods, such as fMRI or PET, which use the haemodynamic response as a measure of cortical activation, can have a temporal-resolution in the range of 4 to 5 seconds (Aine, 1995; Logothetis, 2003). The high-temporal resolution provided allows for the development of a more nuanced understanding of cognitive and neural processes than behavioural measures such as discounting rates and reaction times alone (Luck, Woodman, & Vogel, 2000). EEG recordings also act as a more direct measure of neuronal activity when compared to the hemodynamic responses that fMRI and PET measure (Hari, Parkkonen, & Nangini, 2010).

MEG measures the generation of electric potentials in the brain through the small electromagnetic fields produced by neuronal firing. MEG therefore acts as a measure with the same temporal resolution as EEG, but with improved spatial resolution, as these electromagnetic fields are not dampened by cortical tissue (Hämäläinen, Hari, Ilmoniemi, Knuutila, & Lounasmaa, 1993).

Another key difference between MEG and EEG is that the volume currents from electrical potentials and their resulting magnetic fields are orthogonal in nature; they occur at right angles with each other. The orthogonal nature means that while MEG is optimal for detecting tangential dipoles, EEG is not sensitive to source orientation (Ahlfors, Han, Belliveau, & Hamalainen, 2010) and can detect dipoles of any orientation (Cohen & Cuffin, 1991).

A further advantage of EEG measures is that they are comparatively inexpensive when compared to MEG, fMRI and PET (Schneider & Strüder, 2012).

EEG measures can also be implemented in parallel with other neural measures. For example, MEG and EEG measures can be combined to take advantage of the spatial resolution provided by MEG, as well as the ability to detect all sources provided by EEG (Chowdhury et al., 2015; Ding & Yuan, 2013; Ebersole & Ebersole, 2010; Henson, Mouchlianitis, & Friston, 2009). EEG has also been used in tandem with fMRI to combine the high temporal and spatial resolutions of each method (Huster, Debener, Eichele, & Herrmann, 2012).

While EEG is useful for looking at the temporal dynamics of neural activation, other methods, such as fMRI or MEG, may be appropriate for investigating the spatial aspects of neural activity. As EEG measures electrical activity found on the scalp, this signal has been attenuated by the cortical tissue it has passed through, such as the meninges, cerebrospinal fluid, and skull (Nunez et al., 1997). EEG can localise neural dipoles with an accuracy in the scale of centimetres, meaning it is useful for locating broad regions of activation (Luck, 2005). Neural structures may, however, have several subdivisions, each with their own unique function. For example, while the importance of the OFC in decision making has been emphasised across several areas of research (Padoa-Schioppa & Assad, 2006), very small subdivisions of this area have been reported to act in specific and different ways (Kahnt et al., 2012; Zald et al., 2014).

Further, while source analysis methods allow for the reconstruction of neural sources which may be responsible for the signal found on the scalp, certain identification of this source is impossible. This is commonly called the ‘inverse problem’. The inverse problem means the sources calculated from EEG data may have limited accuracy and may depend on partially inaccurate models of the conductivity

and shape of the head and the cortical tissue that makes it up (Schneider & Strüder, 2012).

2.3 EEG Recordings and Analysis

2.3.1 EEG acquisition

The acquisition of EEG data can be summarised as the recording and measurement of fluctuating scalp potentials over time (Kamp, Pfurtscheller, Edlinger, & da Silva, 2005). Using a conventional EEG method of acquisition, a cap of electrodes is spread across a participant's scalp, and the impedance of the recorded data is reduced using a conducting gel, paste, or liquid. The placement of electrodes should then correspond to a derivative of the *Standardised International 10-20* system, using internationally recognised anatomical landmarks, such as the nasion and inion, with equal distances being kept between all electrodes (Klem, Luders, Jasper, & Elger, 1999; Oostenveld & Praamstra, 2001). Conforming to standardized electrode placements allows for the comparison of data across different labs with different EEG caps.

The electrical signal recorded by the EEG is first digitised for display and analysis purposes. The EEG signal has an amplitude that usually ranges from 10 to 100 μV (Aurlien et al., 2004), which then needs to be amplified to a large degree in order to be accurately measured (Luck, 2005). To accurately record the electrical activity, grounding and reference electrodes must be used. The signal recorded at each electrode is calculated as the difference in voltage between the electrode and a specified reference electrode, or a type of average reference across the whole scalp or a set of selected electrodes (Luck, 2005). Several single electrodes or sets of electrodes can be used as a reference. For example, the mean recordings can be taken from the two electrodes positioned over the bilateral mastoid bones, or the mean recordings

from the entire cap, or the weighted average of the electrodes surrounding the single electrode in question, as is done in Laplacian modelling (Nunez et al., 1997).

The experimental research presented in the current thesis shows data collected from a 128-electrode sponge-based sensor net (Electrical Geodesics Inc, Eugene, Oregon, USA), using a saline solution to connect the electrodes to the scalp. The net was positioned according to three anatomical landmarks: the left and right pre-auricular points and the nasion. The midline Cz electrode was used as a reference, with a sampling rate of 1000 Hz, and was filtered using a band-pass filter between 0.1 to 200 Hz. The high-density system gives good coverage of the participants' heads, with electrodes recording data taken from the face and the inferior head region, not used by caps with fewer electrodes.

Replicability is a core part of the scientific method, to be able to establish consistency of findings across multiple labs and samples. Time-frequency based analyses of electrophysiological data adds several dimensions of complexity to replication attempts. This is because the data is transformed into a multi-dimensional space (time × frequency × electrode × condition), making the replicability of time-frequency data more difficult when compared to other electrophysiological measures such as ERP analyses.

Several steps can be taken to increase the potential replicability of time-frequency analysed EEG data, including ensuring that the experimental design and analysis is clear, and ensuring that proper baseline correction is employed, extending to at least 500 ms before the experimental trial begins (Cohen, 2017). Regarding trial and subject numbers, it is recommended that a minimum of 50 trials and 20 subjects is used in time-frequency analysis to ensure strong effect-sizes (Cohen, 2017). Trial counts should also be matched across experimental conditions, as significant

differences in trial count may lead to effects being found due to signal-to-noise characteristics (Cohen, 2017).

2.3.2 EEG processing

Once a continuous data signal is collected, with triggers included to mark event onset and offset, the EEG data must be processed to be suitable for analysis. The signals collected by EEG electrodes may consist of different forms of activity, some which originate from the brain, some which do not. The electrical signals which do not originate from cerebral sources are defined as artefacts. The source of artifacts can originate from physiological phenomena associated with eye-blinks, movements, muscle activity, and heartbeats (Berg & Scherg, 1994; Ille, Berg, & Scherg, 2002). Non-cerebral artefacts have also been localised to non-physiological sources, such as electrical activity from surrounding devices and wiring, which are generally found in a 50 Hz wavelength (Jung et al., 2000).

While all available steps should be taken to reduce artefacts during data collection, it is inevitable that some artefacts will be found in the subsequent processing phase. The simplest solution for the presence of artefacts in the EEG data is to manually disregard trials containing artefacts using visual inspection. However, this method may cause the loss of a large amount of trials when used to reject stereotyped artefacts which occur commonly throughout the recording sessions.

An alternate method of dealing with artefacts is to use an independent component analysis (Jung et al., 2000), which uses mathematical algorithms to isolate the waveform produced by a specific artefact (such as an EOG or ECG artefact). The component isolated can then be subtracted from the overall waveform to leave a signal more representative of that produced by cerebral sources (Luck, 2005).

The data presented in this thesis was corrected with the adaptive artefact correction method, as analysed in the Brain Electrical Source Analysis software (BESA, GmbH) (Ille et al., 2002). The adaptive artefact correction method uses a spatial filter to separate neural activity from artefacts while avoiding any distortion of the continuous data. Next, artefacts with no stereotyped topography left in the filtered data were manually rejected using visual inspection. Finally, artefacts with a stereotyped topography such as EOG or ECG artefacts were isolated then removed using an independent component analysis method.

2.3.3 Electrode selection

EEG data has a spatiotemporal structure; it is sampled at multiple sensors and timepoints. Because of this, when assessing changes in EEG activity, be it in time-frequency effects or evoked responses, the occurrence of false-positive results being found because of multiple comparisons must be considered. Due to the volume of comparisons being done, EEG analyses can often have many false-positives and lack replicability (Button et al., 2013). For example, 129 electrodes were used in the present data, meaning that if each electrode were analysed separately significant results would be found in 6 to 7 electrodes under randomly produced data.

The traditional solution to this problem is to adjust the significance threshold of the p-value relative to the number of comparisons being made (Maris & Oostenveld, 2007). For example, the Bonferroni correction reduces the significance threshold by dividing it by the number of comparisons being made. However, the limitation of such methods is that they will severely harm the statistical power of research using a high number of comparisons. It may therefore be unfeasible to control the family-wise error rate of EEG data with many electrodes using this method.

The problem of multiple comparisons may instead be solved using nonparametric statistical frameworks, which have been proposed in the analysis of fMRI (Bullmore et al., 1996; Bullmore et al., 1999; Hayasaka & Nichols, 2003, 2004; Holmes, Blair, Watson, & Ford, 1996; Raz, Zheng, Ombao, & Turetsky, 2003) and EEG data (Achim, 2001; Blair & Karniski, 1993; Galan, Biscay, Rodriguez, Perez-Abalo, & Rodriguez, 1997; Guthrie & Buchwald, 1991; Karniski, Blair, & Snider, 1994; Maris, 2004; Maris & Oostenveld, 2007), and have been used successfully in the analysis of frequency-domain representations of EEG and MEG data (Kaiser, Hertrich, Ackermann, & Lutzenberger, 2006; Kaiser & Lutzenberger, 2005; Kaiser, Lutzenberger, Preissl, Mosshammer, & Birbaumer, 2000; Kaiser, Ripper, Birbaumer, & Lutzenberger, 2003; Lutzenberger, Ripper, Busse, Birbaumer, & Kaiser, 2002).

A frequently used non-parametric test is the permutation analysis (Maris & Oostenveld, 2007), which is able to identify electrodes with significant effects without the need for multiple comparisons or the loss of statistical power, as well as providing a data-driven analysis with only minimal a priori assumptions. In a permutation analysis for ERD values, the t-statistics for the main effects and interactions are first calculated across all electrodes and timepoints in specified frequency bands. All the ERD values across conditions are then collated into a single dataset, which is then randomly shuffled, and data points are subsequently drawn from this dataset to form subsets the same size as the previous experimental conditions, electrodes, and time points. This forms a ‘random partition’ representing a dummy version of the experimental variables being investigated, only with data shuffled across the entire dataset. The t-statistics for the main effects and interactions of the experimental variables are then calculated using a random partition. The steps involving the creation and analysis of the random partition is then repeated a set number of times, usually at

least a thousand, and the proportion of random partitions that had larger t-statistics than the initial experimental dataset is taken as the p-value. Electrodes showing significant results and effects of the same direction in the permutation analysis are often clustered based on spatial adjacency (Maris & Oostenveld, 2007).

Cluster-based permutation tests are a popular approach to address the problem of multiple comparisons in MEEG data analysis (Groppe, Urbach, & Kutas, 2011) as they provide high statistical power while controlling for false-positives due to multiple comparisons (Pernet, Latinus, Nichols, & Rousselet, 2015). However, this method of electrode selection may be unsuitable for detecting the spatial boundaries of an effect at the electrode level as no statistical inference is made about individual sensor locations, only the size of effects across whole electrode clusters (Sassenhagen & Draschkow, 2019). In other words, it is inappropriate for researchers selecting clusters of electrodes using this method to make the interpretation that every electrode within a selected cluster must have significant effects or that any electrode not selected does not have significant effects. However, while the boundaries of a cluster at the single electrode level cannot be inferred using a permutation test, it is not inherently wrong to report cluster extents (Sassenhagen & Draschkow, 2019). The general location of an electrode cluster likely overlaps with a true pattern of effects within the EEG data, despite the exact extent of the effect not being apparent when using this test (Sassenhagen & Draschkow, 2019). For this reason, in the research and interpretation portions of the present thesis electrode clusters are only reported regarding their general location, not their exact extents.

The results shown in the present thesis used two thresholding methods to select electrode clusters for further analysis. A permutation analysis was first used, implemented in the *statcond.m* program in the EEGLAB package (Makeig, Delorme,

et al., 2004). The permutation analysis identified clusters of electrodes with significant main effects or interactions according to a pre-defined significance threshold ($p = .01$). The permutation test was able to control for the inflation in type-1 error probabilities due to multiple comparisons by assessing main effects and interactions within the data, comparing effects using the data collected by every sensor in the 129-electrode array without a loss in statistical power.

Second, due to the spatial impreciseness of cluster-based permutation analyses, only electrodes with consistent ERD/ERS effects were considered in subsequent analyses. To ensure electrodes with consistent ERD/ERS effects were selected, T-tests with significance thresholds of .01 were used to test whether changes over each electrode were significantly different from 0. Electrode clusters which passed both the permutation and the difference from 0 tests were selected for further analysis, done in SPSS v. 22 (IBM Inc., USA).

2.4 Time-frequency Analysis

As well as being described as phase-locked evoked responses to events, EEG activity can also be described in terms of power changes within specific frequency bands (Steriade, 1999). A common method to analyse the rhythmic activity found within neural oscillations is to describe activity in terms of changes in the power within specific oscillatory frequency bands (Steriade, 1999).

When analysing frequency effects, EEG data is commonly split into specified frequency bands, with lower frequency bands generally exhibiting larger amplitudes than higher ones (Niedermeyer, 2005). Once the data has been split into specified frequency bands, changes in power in these bands in response to specific conditions and events can be investigated.

When conducting a time-frequency analysis, a time-domain signal must be deconstructed into its constituent oscillatory components. There are many approaches to the decomposition of oscillatory data, including simple band-pass filters (Herrmann, Grigutsch, & Busch, 2005) the short-term Fourier transformation (Gabor, 1946), and continuous (Combes et al., 2012; Daubechies & Bates, 1993) or discrete (Mallat, 1989) wavelet transformations. The common principal behind these differing approaches is that time-frequency decomposition methods all require a trade-off between temporal and frequency resolution (Roach & Mathalon, 2008). This trade-off occurs because, as the time-window used to estimate time-frequency data gets larger, the higher the frequency resolution but the lower the temporal resolution, and vice-versa (Roach & Mathalon, 2008).

Fourier transformations, or the similar Welch power method, are usually performed in a short-time window that is shifted across the time series data to identify changes in the power of EEG signals in a specified frequency range over time (Roach 2008). The choice of shifting time-windows in this decomposition method constrains the size of the frequency bin used, which must be uniform across all frequencies. (Roach 2008).

Continuous wavelet transformations encompass a class of spectral decomposition methods which represent a more flexible alternative to the windowed short-term Fourier analysis (Herrmann et al., 2005; Roach & Mathalon, 2008; Samar, Bopardikar, Rao, & Swartz, 1999). Wavelet transformations deconvolve oscillatory components using compressed and stretched versions of the “mother wavelet” (e.g., the Morelet wavelet) to fit each frequency being extracted from the EEG signal, which is traditionally constrained to contain the same number of cycles across frequencies (Herrmann et al., 2005; Roach & Mathalon, 2008; Samar, Bopardikar, Rao, & Swartz,

1999). As a result, wavelet analyses utilizes a different time-window length depending on the frequency of the signal being assessed, with longer time windows being applied to slower frequencies. The variation in time-window length causes finer temporal resolution as frequency increases at the cost of poorer frequency resolution (Herrmann et al., 2005; Roach & Mathalon, 2008; Samar, Bopardikar, Rao, & Swartz, 1999). Further, for high-frequency signals, it is often assumed that Morelet wavelet decomposition provides greater temporal resolution, but poorer frequency resolution than short-term Fourier decomposition (Roach & Mathalon, 2008).

Oscillations at frequencies not sampled in the Fourier or wavelet transformation may spread their energy to the sampled frequencies, which is commonly referred to as spectral leakage. Spectral leakage usually occurs because of how the data is tapered, where if the edges of a sampled frequency do not fit into the specified time-window, they are tapered into other frequencies. The shape of the tapers used must therefore be modified based on the size of the time-window and the frequencies being investigated. The Hanning window is a taper formed by using a weighted cosine function, smoothing discontinuities at the edges of the sampled frequency (Blackman & Tukey, 1958; Kanasewich, 1981; Press, Teukolsky, Vetterling, & Flannery, 1992). Alternately, multiple tapers can be used. Multiple tapers are typically used to achieve better control over the level of frequency smoothing which are then averaged together, and are recommended for slower frequency bands (Klimesch, 2012a).

2.4.1 Cortical rhythms and their generators

Traditional views of neural function describe brain activity as being driven by functional anatomy. However, for a more comprehensive account, the temporal structure of cortical activity must also be considered. The temporal structure of cortical

activity can be assessed through changes in neural activity oscillating at different frequencies (Arnal & Giraud, 2012; Buzsáki & Draguhn, 2004; Chakravarthi & Vanrullen, 2012).

Early studies described activity occurring within specific frequency bands as being generated by networks of discrete cortical structures (Andersen & Andersson, 1968; Speckmann et al., 2011). More recent research, however, has described frequency-specific activity as originating from interactions between cortical structures of different sizes, rather than the activation from cortical structures themselves (Klimesch, 2012a).

There are several factors which determine the properties of EEG oscillations (Singer, 1993). The first is the intrinsic membrane properties of the neurons being activated and the resulting dynamics of post-synaptic firing, including the rate of firing and the strength of the interconnections between individual neurons. A second factor is the strength and extent of the interconnections between larger cortical networks, especially when considering slower frequency activation such as that in the theta band (Izhikevich & Edelman, 2008; Robinson et al., 2001; Steriade, 2000).

The frequency of electrical oscillations found on the scalp is thought to be dependent on the number of synchronously activated neurons. Slower frequencies, such as alpha- and theta-band activations, have been associated with a large area of synchronous activation (Kopell, Ermentrout, Whittington, & Traub, 2000; Miller, 2007; Singer, 1993; von Stein et al., 2000) or the underlying excitation-inhibition balance of cortical areas (Brunel & Wang, 2003; Jensen & Lisman, 2005; Whittington, Traub, Kopell, Ermentrout, & Buhl, 2000). Conversely, faster frequency bands, such as the beta band, has been associated with a much smaller pattern of activation and more specific processing of information (Klimesch, 1996).

2.4.2 ERD methods

Time-frequency changes in relation to specific events are often investigated using an ERD/ERS methodology. An ERD is defined as a relative decrease in power in a specified frequency band following an event (Pfurtscheller, 1977), whereas an ERS is defined as a relative increase in power (Pfurtscheller & Lopes da Silva, 1999). ERD/ERS changes are usually quantified as a percentage compared to a baseline period seconds before the event using the ERD transformation. The equation for this transformation is presented below:

$$\mathbf{D}\boldsymbol{j} = \frac{\boldsymbol{Pj} - \boldsymbol{R}}{\boldsymbol{R}} \times \mathbf{100}$$

Where $\mathbf{D}\boldsymbol{j}$ is the ERD output within a specific time series sample (j), P_j is the absolute power at time sample j, and R is the mean power over the baseline period (Pfurtscheller & Aranibar, 1977).

The ERD and ERS of specific frequency bands typically accompanies events such as somatosensory stimulation (Chatrian et al., 1959; Pfurtscheller, 1981) and motor activation (Neuper & Pfurtscheller, 2001a; Pfurtscheller, Neuper, & Kalcher, 1993; Stancak & Pfurtscheller, 1996; Stancak et al., 1997). In these contexts, ERD in the alpha and beta bands is typically interpreted as reflecting cortical activation or preparation (Pfurtscheller & Lopes da Silva, 1999), an interpretation supported by the correlation found between ERD changes in these bands and an increase in the BOLD-fMRI signal (Babiloni, Vecchio, Bultrini, Luca Romani, & Rossini, 2005; Formaggio et al., 2008; Mantini, Perrucci, Del Gratta, Romani, & Corbetta, 2007; Singh, Barnes, Hillebrand, Forde, & Williams, 2002). To increase the statistical reliability of the results, ERD/ERS values are averaged over trials and time intervals, with increased

trials and longer time-windows increasing reliability. In typical analyses, ERD is averaged over a minimum of 30-80 trials with a time-window of at least 125-250 ms (Formaggio et al., 2008).

For the quantification of ERD/ERS changes relating to limb movements, it is recommended that a common average reference or a reference-free Laplacian transformation is used (Pfurtscheller, Flotzinger, & Neuper, 1994). Common average referencing uses the mean activation collected from all electrodes across the scalp as the reference, thus restoring the signal at the reference electrode used during recording. The advantage of this referencing method is that it does not depend on the activity from any single source and creates a more spatially dispersed referencing effect (Pfurtscheller et al., 1994). Laplacian modelling is used to remove reference effects from EEG data by using a unique reference for each electrode, taken as the average activity from the surrounding electrodes (Pfurtscheller et al., 1994). Laplacian modelling acts as a spatial filter, attenuated to the volume conducted influence of more remote sources and enhancing the spatial resolution of currents flowing perpendicular to the electrode (Pfurtscheller et al., 1994).

2.4.3 ERD effects investigated in this thesis

Amplitude suppressions and enhancements in the alpha, beta and theta frequency bands are commonly associated with a range of external stimuli and cognitive states. Alpha rhythms describe EEG frequencies which occur within the 8-12 Hz range (Niedermeyer, 2005), and typically have an amplitude ranging up to 50 μV, which is strongest over parietal, posterior temporal, and occipital areas of the scalp (Niedermeyer, 2005). Beta-band oscillations are those which occur within the 16-30 Hz frequency range (Miller, 2007), and usually occur with amplitudes below 30 μV, broadly distributed across the scalp (Niedermeyer, 2005). Finally, theta rhythms

describe oscillatory frequencies within the 4-7 Hz range (Schacter, 1977), which are more broadly distributed across the brain than alpha and beta rhythms (Raghavachari et al., 2006).

EEG recordings for the present thesis were taken during the sustained vigilance and Go/NoGo tasks. ERD was calculated in the anticipation period between the occurrence of the cue and the target stimulus and investigated in the alpha (8-12 Hz), beta (16-24 Hz) and theta (4-7 Hz) frequency bands. The patterns of activation taken were hypothesised to represent preparatory motor or inhibition responses, as well as anticipatory attention and tonic effortful engagement.

Patterns of ERD/ERS in the specified frequency bands were considered regarding how they were modulated by differing incentives (chapters 4, 5 and 6), how they differed preceding fast compared to slow responses (chapters 4 and 5) and how they were modulated by Go/NoGo motor primes (chapter 6).

The core measure of interest across the research chapters was how incentives of differing magnitudes and valence differentially modulated patterns of ERD/ERS representing preparatory motor activation and inhibition, as well as anticipatory attention and tonic effortful engagement. Further, as these processes were considered to be the mediating factor between incentive and effortful performance, it was hypothesised that ERD/ERS effects modulated by reward, especially those in the beta band, would be stronger when preceding a fast compared to a slow response. The correlations between ERD/ERS effects and measures of effortful performance (Go-RTs and NoGo stopping rates) were also assessed, as well as the relation between individual discounting rates and cortical/behavioural changes under differing incentives. Finally, to investigate the interaction between

approach/avoidance motor-sets and incentive valence, ERD differences between Go and NoGo motor prime conditions were considered.

Chapter 3 – Research Problems and Hypotheses

3.1 Research Problems

The brain structures underlying effortful engagement and decision making are well understood (Kool et al., 2010; Botvinick, Niv, & Barto, 2009), and the effects of different kinds of incentive on effortful behaviour have been shown (Chong et al., 2017; Massar et al., 2015; Padmala & Pessoa, 2011; Carsten, Hoofs, Boehler, and Krebs 2018). In contrast, the way cortical processes interact during effortful engagement has received less attention. Namely, it is unclear what effect differing incentives have on effortful processes during engagement, and why the motivational value of incentives so often diverges from their effect on effortful performance

There are several unanswered questions regarding the effect of incentives on effortful deployment and the associated cortical processes. First, cognitive effort has been posited to be reflective of a process of strategic cortical activation and inhibition, leading to an opportunity cost of effort (Lazarus, 1993; Tooby & Cosmides, 2008). However, the contrasting activation and inhibition processes associated with effortful engagement have yet to be demonstrated, and the way incentives of differing magnitudes modulate these processes requires further elucidation. Second, monetary losses are often found to be more motivating than gains (Baumeister, Bratslavsky, Finkenauer, & Vohs, 2001; Rozin & Royzman, 2001) but often result in no difference in effortful performance (Boksem et al., 2008; Maruo et al., 2016; Seifert et al., 2006), or even a deterioration in effortful performance (Hagger et al., 2010; Paschke et al., 2015; Potts, 2011) relative to gains of equal nominal value. Due to the different valuation processes employed by gains and losses, it is unclear whether they modulate similar cortical processes when used as incentives during effortful engagement.

Further, the underlying cause of the divergent effect of gains and losses on effortful performance is yet to be explained, although it has been hypothesised to be due to approach/avoidance associations and attentional biases made in response to gains and losses. Finally, cognitive effort is hypothesised to be deployed proportional to the SV of offered rewards (Bialaszek et al., 2017; Ostaszewski, Bąbel, & Swebodziński, 2013; Sugiwaka & Okouchi, 2004), however the association between the SV of reward relative to effortful engagement under differing incentives has yet to be investigated.

The research presented in the current thesis measured changes in ERD/ERS in the alpha, beta, and theta bands while participants expected a target stimulus during a sustained vigilance task or a cued Go/NoGo task using monetary gains and losses as incentives. ERD found during these tasks reflected the anticipatory processes associated with the task, such as cortical inhibition, motor preparation, and anticipatory attention. Expanding on this, we used a COGED task to investigate individual discounting rates in gain and loss modalities, and correlated discounting rates with changes in effortful performance and anticipatory ERD/ERS with differing incentive types.

3.2 Hypotheses

H1 Graded incentives will be associated with increased anticipatory ERD in the alpha and beta bands over sensorimotor areas, and ERS in the beta band over right-frontal areas, as well as a stronger ERS in the theta-band over parieto-frontal areas during a sustained vigilance task.

H2 Similarly, a significantly stronger ERD in the alpha and beta bands will be found over sensorimotor areas, and a stronger beta-band ERS will be found

over right-frontal areas of the scalp when preceding fast compared to slow responses.

H3 Individual SVs of cognitive effort discounting will be significantly associated with changes in RTs and ERDs, showing that participants who show smaller effort-based reward discounting will be more motivated by incentives to engage effortful resources.

H4 Losses will be more motivating than gains in the COGED task, however, when losses are used as graded incentives, they will show symmetrical effects on response-speeds and cortical responses during the sustained vigilance task.

H5 In a Go/NoGo task, losses and inhibitory motor sets will be associated with a relative deterioration in anticipatory attention, as reflected by weaker alpha-band ERD over frontal- and posterior parietal regions of the scalp compared to gains of equal nominal value.

3.3 Thesis chapters

Chapter 4 describes two experiments which investigated how reward levels interacted with effortful engagement using measures of task- and baseline-dependent patterns of cortical inhibition over frontal regions and cortical activation in sensorimotor regions during a sustained vigilance task (H_1). The two experiments described in chapter 4 also used a COGED procedure to measure individual effort-discounting rates, and assed how well these correlated with cortical and behavioural responses to reward (H_2).

Chapter 5 examines the effect of graded losses and gains on effortful performance and preparatory motor activity during a sustained vigilance task. Using these methods, the effect of losses and gains on response-speeds and ERD modulations were modelled as quadratic and linear trends, and the slopes of losses and gains were compared (H_3). Similar to the experiments described in chapter 4, a COGED procedure was used, although one which included both losses and gains (H_3). Using this procedure, the individual SVs of losses and gains could be compared, and the relationship between SVs and changes in response-speed and cortical preparation with rewards and losses could be assessed (H_2).

Chapter 6 discusses an experiment expanding on the methodology of the previous three, using a cued Go/NoGo task rather than a sustained vigilance task. Gain, loss, and no incentive reward conditions were included, as well as two 'prime' conditions where participants either expected an approach motor response or an inhibitive response with a probability of 0.75. This methodology allowed us to directly compare whether the differential effects of gains and losses on cortical activation associated with effortful performance showed overlapping effects to task-induced approach and avoidance tendencies (H_4). The individual SVs of effort under losses and gains, and its relationship to behavioural and cortical changes were also assessed (H_2).

Chapter 7 comprises a general discussion of all experimental findings. The implications of the findings are discussed in the context of the current opinions in the field of neuroeconomics, and future directions are deliberated.

Chapter 4
The cortical oscillatory patterns associated with varying levels of reward during an effortful vigilance task.

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This experiment investigated changes in cortical oscillatory power in the alpha, beta, and theta bands during effortful engagement under rewards of different magnitudes.

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The format of the text has been modified to match the style of this thesis.
The roles of the co-authors are summarised below:
I designed the study in collaboration with Andrej Stancak and collected the data. Katerina Kokmotou, Hannah Roberts, Vicente Soto, John Tyson-Carr, and Danielle Hewitt assisted with the collection of data and contributed useful comments whilst preparing the manuscript for publication. Andrej Stancak, and Timo Giesbrecht contributed to the experimental design as well as the large-scale planning of this project. Andrej Stancak and Timo Giesbrecht secured funding for project.

4.1 Abstract

We explored how reward and value of effort shapes performance in a sustained vigilance, reaction time (RT) task. It was posited that reward and value would speed up responses and increase cognitive effort by boosting activation in the sensorimotor cortex and

increasing inhibition in frontal cortical regions, similar to the horse-race model of motor actions.

Participants performed a series of speeded responses while expecting one of three monetary rewards (0 pence (p), 1p, and 10p) if they responded faster than their median RT. Amplitudes of cortical alpha, beta, and theta oscillations were analysed using the event-related desynchronization method. In experiment 1 (N = 29, with 12 females), the reward was consistent within each block; while in experiment 2 (N = 17, with 12 females), reward amount was displayed before each trial. Each experiment evaluated the baseline amplitude of cortical oscillations differently. The value of effort was evaluated using a cognitive effort discounting task (COGED).

In both experiments, RTs decreased significantly with higher rewards. Reward level increased the amplitude of beta-band oscillations over frontal electrodes in experiment 1. In experiment 2, reward decreased the amplitudes of beta oscillations in the ipsilateral sensorimotor cortex. Individual effort values did not significantly correlate with oscillatory changes in either experiment.

Results demonstrate that the amount of expected reward during a sustained vigilance task modulates activation in the ipsilateral sensorimotor cortex (experiment 2) and inhibition in the frontal cortex (experiment 1), and that while individual economic value changes the willingness to accept effortful participation, it does not shape RTs or cortical activation patterns.

4.2 Introduction

Cognitive effort is prevalent in a number of settings such as education (Cacioppo, Petty, Feinstein, & Jarvis, 1996; Von Stumm, Hell, & Chamorro-Premuzic, 2011), the workplace (Kidwell Jr & Bennett, 1993; Van Iddekinge, Aguinis, Mackey, & DeOrtentiis, 2018), and consumer behaviour (Heidig, Wentzel, Tomczak, Wiecek, & Faltl, 2017). In psychiatric or mood disorders (e.g., depression), a loss of motivation to face cognitively or physically challenging tasks has been reported (Cohen et al., 2001; Treadway et al., 2012). However, while the decision to make an effort has been extensively researched, and the subjective experience of effort is familiar to most people, the effects of reward and the value of effort on performance in an effortful task and the neural basis of this are not yet fully understood.

In behavioural economic theories of decision making, effort is framed as a discounting factor that reduces the value of rewards when an effort is required to achieve them (Inzlicht et al., 2014; Kurzban et al., 2013). The discounting effect of effort can be measured using the COGED method (Westbrook & Braver, 2015; Westbrook et al., 2013), which offers staircase iterated rewards across multiple levels of effort until an indifference point is reached, indicating the amount of money required for participants to agree to put more effort into the task (Massar et al., 2016; Westbrook et al., 2013). The value of effort, determined using COGED, has been shown to correlate with individual engagement (Westbrook et al., 2013) and performance (Massar et al., 2016) in cognitive tasks. Further, the level of engagement in a cognitive task can be manipulated by varying performance-based rewards (Dinges & Powell, 1985; Knutson et al., 2000; Massar et al., 2016).

The discounting effect of cognitive effort has been attributed to a number of processes (Christie & Schrater, 2015; Gailliot & Baumeister, 2007; Lazarus, 1993;

Tooby & Cosmides, 2008), but is commonly thought to be the consequence of top-down cognitive control (Botvinick & Braver, 2015; Kaplan & Berman, 2010; Shenhav et al., 2013b). This would be required to control task-relevant cortical activation and inhibition at the expense of task-irrelevant activation and inhibition, and may be localised to the dorsal anterior cingulate cortex, which has been implied to mediate cognitive control during attentional tasks (Shenhav et al., 2013a).

Processes which may to be controlled during motor actions are proposed by the horse-race model of motor inhibition in the stop-signal task (G. P. Band, Van Der Molen, & Logan, 2003; Logan & Cowan, 1984; Schultz, 2015). This model posits opposing processes of motor readiness during stop-signal tasks, where motor activation occurs in response to a 'GO' signal and motor inhibition occurs in response to a 'STOP' signal, and a movement is only successfully inhibited if the inhibitive processes complete before the movement is finished, meaning that successful responses to 'STOP' signals are based on the relative speed of these competing processes (for more information see Band et al. 2003, Figure 4.1).

Visual acuity (Kyle E Mathewson, Gratton, Fabiani, Beck, & Ro, 2009), visual detection threshold (Ergenoglu et al., 2004), visual discrimination (Hanslmayr et al., 2005) and pain sensitivity (Babiloni et al., 2006) have been shown to be enhanced if stimuli occurred during a period of suppressed alpha-band oscillations. In a similar vein, motor readiness or preparation seconds before a self-paced voluntary movement (Chatrian et al., 1959), or during an imagined, or observed movement (Nagai & Tanaka, 2019; Pfurtscheller et al., 2005), often manifests in amplitude decreases of cortical alpha- and beta-band oscillations (Fox et al., 2016; A. Ishii et al., 2019; Pfurtscheller & Berghold, 1989; Rhodes, 2019; Charidimos Tzagarakis et al., 2010; C. Tzagarakis et al., 2015). This has been found to increase prior to self-paced finger

movements requiring large force (A. Stancak et al., 1997), and during fast compared to slow movements (A. Stancak, Jr. & G. Pfurtscheller, 1996; A. Stancak & G. Pfurtscheller, 1996). Suppressions of alpha- beta-band band power may, therefore, be representative of the excitatory processes posited by the horse-race model of motor actions.

Conversely, inhibitory processes are employed in tasks which require withholding a response under the state of strong motor readiness, for example during a stop-signal task (Leimkuhler & Mesulam, 1985). Cortical inhibition or idling has been found to manifest as an increase in the amplitude of alpha- or beta-band oscillations (Adam Fry et al., 2016; Jensen et al., 2005; Korzhik, Morenko, & Kotsan, 2018; G. Pfurtscheller, A. Stancak, Jr., et al., 1996; Salmelin & Hari, 1994; Visani et al., 2019), and frontal beta-band synchronisation has been shown to occur during periods of motor inhibition (Alegre et al., 2006; Fonken et al., 2016; Swann et al., 2009; Wagner et al., 2018; J. R. Wessel & Aron, 2013). Functional brain imaging studies point to a major role of the right prefrontal cortex in employing the inhibition of motor actions (Feng, Schwemmer, Gershman, & Cohen, 2014; H. Garavan, Ross, Murphy, Roche, & Stein, 2002; Simmonds, Pekar, & Mostofsky, 2008), perhaps through dopaminergic innervations (Chao & Knight, 1995; Fuster, 2015; Miller & D'Esposito, 2005). Moreover, frontal beta-band synchronisation has been shown to occur during periods of motor inhibition (Alegre et al., 2006; Fonken et al., 2016; Swann et al., 2009; Wagner et al., 2018; J. R. Wessel & Aron, 2013). These areas may be expected to show an increase in alpha- and beta-amplitudes during increased motor inhibition, representing a temporary withholding of movement under the state of high motor readiness.

Theta-band oscillations, in contrast, have been found to increase over mid-frontal electrodes during periods of sustained attention (Angelidis, Hagenaars, van Son, van der Does, & Putman, 2018; Basar-Eroglu, Basar, Demiralp, & Schurmann, 1992; Wolfgang Klimesch, 1999; Rajan et al., 2018), and have been hypothesised to be a correlate of cognitive effort or fatigue (Arnau, Mockel, Rinkenauer, & Wascher, 2017). We, therefore, assumed that oscillatory power in the theta band may be involved in the attentional, or top-down processes required during effortful tasks.

The present study combined a modified sustained vigilance task (Massar et al., 2016) with a monetary incentive delay task (Knutson et al., 2000) to examine the effects of varying levels of rewards and the value of effort on cortical activation and inhibition. The vigilance task required participants to execute speeded reaction-time (RT) responses during a stream of visual cues occurring in short iterations, and it has been shown that requiring participants to complete a sustained vigilance task, with each block offering different rewards (no reward, low reward, or high reward) for each fast response (faster than the participant's median RT) results in reward-related changes in task performance and sympathetic arousal (Massar et al., 2016), however the effects of reward on cortical oscillatory activity during this task has not yet been investigated.

Experiment 1 aimed to analyse the change in amplitudes of cortical alpha, beta, and theta oscillations in the time-window just preceding the cue prompting a speeded response during a vigilance task, and to test whether individual subjective values of effort, evaluated using a COGED method, would correlate with performance and cortical oscillatory changes. Stimuli were presented in three blocks, with each differing in the incentive for fast responses (0p, 1p, 10p), and EEG data was recorded over a 90-s time window preceding each block to take the baseline into account during the

calculation of relative-band power (RBP). Due to this block design, and as participants did not know when the target stimulus would occur, a constant state of motor activation was required, meaning a greater likelihood of observing a modulation of inhibition in cortical oscillatory changes was expected, as the release of inhibition would be required for movement. We therefore hypothesised that reward and response-speed would modulate sensorimotor alpha-band and frontal beta-band synchronisation, with stronger synchronisation being found preceding fast trials and in larger reward blocks, representing stronger inhibition.

Since the type of baseline employed in experiment 1 cannot fully account for fast changes in arousal and motivation occurring during a lengthy vigilance task, experiment 2 was carried out to analyse the effect of reward on cortical activation in a vigilance task using a standard event-related desynchronization (ERD) paradigm (Pfurtscheller & Aranibar, 1977). The time course of the relative band power changes was analysed in a period of time, seconds before each trial. Trials involving no reward (0p), a small reward (1p) and a high reward (10p) were presented in a random order, with a visual cue 2 seconds before the stimulus prompting a speeded response. In this experiment, we aimed to measure the cortical processes associated with motor activation. As the participants knew when the target stimulus would occur, we predicted fast response-speeds and higher rewards would be associated with stronger alpha- and beta-band ERD over sensorimotor regions, as well as stronger theta-band synchronisation over central frontal regions. We also predicted, in both experiments, that participants who showed less effort-discounting in the COGED task would show stronger changes in RT and ERD/RBP as a function of reward.

4.3 Methods

4.3.1 Experiment 1

4.3.1.1 Participants

29 subjects (12 females) were recruited. Five subjects were removed from subsequent EEG analysis due to excessive muscle artefacts. Therefore, the final sample included 24 participants (10 females), aged 23.34 ± 2.44 (mean ± SD). The procedure used was approved by the Research Ethics Committee of the University of Liverpool and all participants gave fully informed written consent at the start of the experiment in accordance with the Declaration of Helsinki.

4.3.1.2 Procedure

Participants were required to complete two tasks. The participants first completed a modification of the sustained vigilance tasks used by Massar et al. (2016) and Dinges and Powell (1985), while EEG was recorded. The second task was a short discounting task requiring the participants to make a series of 36 choices between a high-effort, high-reward option and a low-effort, low-reward option. The purpose of this task was to estimate the subjective value (SV) attributed to each level of effort offered during the task and to evaluate individual indifference points equalling monetary value and units of effort

The vigilance task consisted of 1 five-minute practice block with no EEG recordings and 3 ten-minute experimental blocks with EEG recordings included. The five-minute block consisted of 50 trials, and each ten-minute block consisted of 100 trials. Overall, the participants completed 350 trials throughout the experiment. Participants were offered different rewards for each fast response in each block (0p, 1p, or 10p), and feedback regarding the amount of money and number of points the participants had currently earned was given after each block. Effort was measured

behaviourally using the participants' mean RTs and electrophysiologically using the participants' change in RBP in the 1-s epoch preceding the presentation of the target stimulus and during the 90 second baseline period of each block.

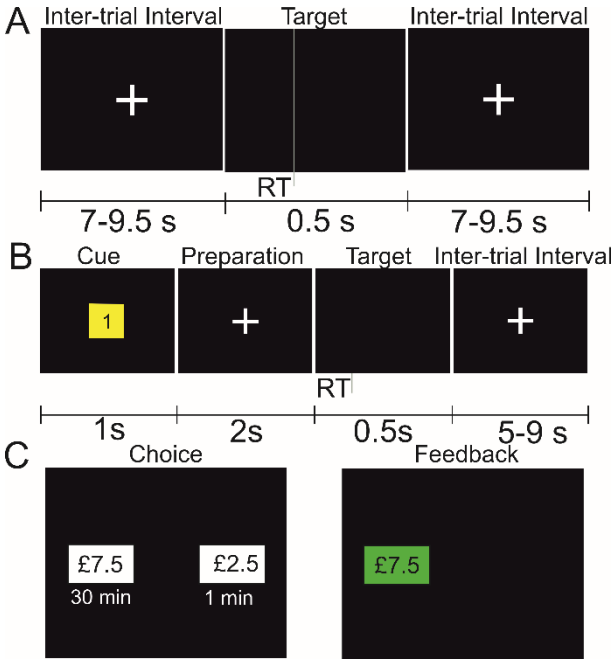


Figure 4.1. A schematic representation of trials presented to participants in the motivated vigilance task for (A) experiment 1 showing first the inter-trial interval, then the target stimulus, followed by the inter-trial interval for the following trial; (B) experiment 2, showing first the cue stimulus, then the period of preparation, followed by the target stimulus; and, finally the inter-trial interval, and (C) the discounting choice task for both experiments, showing, first an example choice offered to the participants, followed by feedback confirming the selected choice.

4.3.1.3 Sustained vigilance task

The sustained vigilance task was an adaptation of the Psychomotor Vigilance Test used by Dinges and Powell (1985). This was a 10-minute sustained attention task in which participants were required to respond with a button press (left mouse button) with their right hand as quickly as possible whenever they are presented with a target stimulus. The scheme of the vigilance task is shown in Figure 4.1A.

After the application of the EEG net, participants were taken into a dimly lit, sound attenuated room and were asked to complete the sustained vigilance task.

Participants were seated in front of a 19-inch CRT monitor and used their right hand to make responses on a computer mouse. The stimuli were presented using Cogent 2000 software (UCL, London, United Kingdom) for Matlab R2016b. (Mathworks, Inc., USA).

Participants were presented with a white fixation cross in the centre of a black screen monitor. The target stimulus occurred when the fixation cross disappeared for 0.5 seconds. The presentation of the target stimuli was separated by uniformly distributed inter-trail intervals which ranged from 3.5 to 9 seconds. Participants first completed a five-minute practice run of the task with no rewards offered. During this baseline run the participants' median RT was calculated, which was then used as the target RT in the following 3 ten-minute blocks.

Following the practice block, participants were required to complete three experimental ten-minute blocks of the same task. In one of the experimental blocks the participants were not offered any reward and were instructed to respond as quickly and as accurately as possible whenever the target stimulus occurred, and in the other two experimental blocks the participants were offered a monetary reward whenever they responded to the target stimulus faster than, or as fast as, their previously calculated median RT. In one of these two blocks participants were offered 1p per fast response and were offered 10p per fast response in the other block. Participants were presented with 100 target stimuli in each block, meaning they were offered a total of £1 or £10 in the two reward blocks respectively if they received the reward on every trial. In order to prevent practice or fatigue effects the order of the three experimental blocks was randomly generated by a computer at the start of each experiment, and a one-sample chi-square test was conducted to check the transitional probability of block

order, confirming that any block order was not presented significantly more often than the others ($p = .40$).

EEG recordings were acquired throughout the study. At the start of each of the three blocks, a 90-second baseline period was recorded, during which participants were instructed to look at the fixation cross presented on the monitor. The cross would not disappear and the participants were not required to make a response.

Trials were split in half based on whether participants responded faster than their median RT were encoded as fast trials and trials where participants responded slower than their median RT were encoded as slow trials. Behavioural measures of attention were taken as being the mean RT for each participant in each experimental block (0p, 1p, 10p) and response-speed trials (fast and slow).

4.3.1.4 Discounting task

The discounting task (Massar et al., 2016; Westbrook et al., 2013) was used to evaluate subjective costs of six levels of effort (5, 10, 15, 20, 25, and 30 minutes) for each participant using a series of monetary decisions.

Participants were first told that they would be required to complete the previous sustained vigilance task again for an amount of time (ranging from one minute to thirty minutes) based on the choices made in the discounting task.

Following this, participants were presented with 36 pairs of monetary offers, with each pair always consisting of one low-effort, low-reward option, and one high-effort, high-reward option (Figure 4.1C). The low-effort option always required participants to complete the task again for only one minute, whereas the amounts of time given in the high-effort option was varied based on which condition the trial was in. Participants were offered a fixed reward of £12 in the high-effort option in every trial. In comparison, the reward offered for the low-effort option was adjusted

following a staircase titration method (i.e., the offer was increased if the high effort option was chosen and decreased if the low effort option was chosen). The participants were first offered £6 for the low-effort choice with an extra £2.50 being added to, or taken away from, this amount depending on participant choice. The amount of money added to, or taken away from, the low-effort option was then halved each time the participant made a decision. The participants made six choices during each effort block (5, 10, 15, 20, 25, 30 minutes), and the order of conditions was randomly presented for each participant.

Following the final choice, one trial was randomly chosen through the generation of a random number between 1 and 36, which would then refer to the chosen trial number. Next, the participant would be required to complete the vigilance task for the amount of time chosen during the selected trial and would receive the amount of money associated with that choice.

An indifference point was calculated for each condition, and used as a measure of the subjective value of effort. This was defined as the average of the largest low-effort monetary offer for which the participant chose the low-effort option, and the lowest low-effort monetary offer for which the participants chose the high-effort option (Massar et al., 2016; Westbrook et al., 2013).

In order to control for temporal discounting, participants were informed that they would be required to remain in the laboratory for the full 30 minutes in total, including the time spent completing the task. This ensured that the participants made decisions during the discounting task based upon the effort required rather than the time taken to complete the task. The boredom associated with remaining in the laboratory was not explored directly, however all participants discounted higher levels (30 min) more than lower levels (5 min).

The area under the curve (AuC) in the function representing associations between units of efforts and requested payoffs was computed in every participant (Myerson et al., 2001). This measure corresponds to SV of effort and has been found to be correlated with need for cognition scores (Westbrook et al., 2013). A Bivariate correlation was conducted to assess the relationship between this function to RTs and RBP values.

4.3.1.5 EEG recordings

EEG data was recorded continuously using a 129-channel Geodesics EGI System (Electrical Geodesics, Inc., Eugene, Oregon, USA) with a sponge-based HydroCel Sensor Net. The net was aligned with reference to three anatomical head landmarks: two preauricular points and the nasion landmark. Electrode-to-skin impedances were kept below 50 kΩ and were kept at equal levels across all electrodes. A recording band-pass filter was set at 0.001-200 Hz with a sampling rate of 1000 Hz. The Cz electrode was used as a reference electrode.

4.3.1.6 Spectral analysis of EEG signals

EEG data was pre-processed using BESA v 6.1 (MEGIS GmbH, Germany). EEG signals were re-referenced using a common average reference method (Lehmann, 1984) which restored the signal at electrode Cz. Eye blinks and electrocardiographic artefacts were removed using principal component analysis (Berg & Scherg, 1994). Further, data were visually inspected for the presence of any movement or muscle artefacts, and epochs contaminated with artefacts were excluded from subsequent analysis.

While participants completed all trials behaviourally, the average number of trials accepted for EEG analysis in each condition was: 0p, 53.9 ± 14.0 (mean ± SD);

1p, 54 ± 15.5 (mean ± SD); 10p, 55.8 ± 14.3 (mean ± SD). The average number of accepted trials did not differ across conditions ($p > 0.05$). A recording band-pass filter was set at 0.001-1000 Hz with a sampling rate of 1000 Hz.

Continuous EEG data was split into two sets of 1-second epochs. One set of epochs comprised epochs preceding the disappearance of the fixation cross (-1.0 - 0.0 s). This set of epochs was uses to evaluate the cortical activation preceding the speeded RT response. The other set of 1-s epochs was selected from the 90-second resting period which was recorded at the start of each block. All artefact-free 1-second non-overlapping epochs were used. This set of epochs was used to evaluate the baseline amplitudes of cortical oscillations and was used further to evaluate RBP changes.

EEG signals were down-sampled to 256 Hz. In both epochs, the power spectra were computed in Matlab (The Mathworks, Inc., USA) using Welch's power spectral estimate method. All epochs comprising one set of epochs were aligned to form a quasi-continuous EEG signals. The power spectral densities were computed from non-overlapping 1-second segments (256 points). Each data segment was smoothed using a Hanning window. The power spectral densities were estimated in the range 1-80 Hz with a frequency resolution of 1 Hz.

The RBP in the alpha (8-12 Hz), beta (16-24 Hz) and theta (4-7 Hz) bands were evaluated in each of three conditions using the classical ERD transformation (Pfurtscheller & Aranibar, 1979):

$$\boldsymbol{D = \left(100 * \frac{R - A}{R}\right)}$$

Where D represents the RBP during epochs preceding the disappearance of the fixation cross (A) relative to the rest condition (R). Positive values of D correspond to the relative band power decreases which are considered to signify the presence of

cortical activation. In contrast, negative D values refer to the amplitude increases of band power or cortical synchronisation.

4.3.1.7 Statistical analysis

The differences in the median RT across three blocks and two speed conditions of the vigilance task were compared using a 2×3 repeated measures ANOVA with three levels of reward (0p, 1p and 10p) and two levels of response-speed (fast and slow). As participants were rewarded based on whether they beat their median RTs, the two levels of response speed were an integral part of the experimental procedure. These were included in this analysis to confirm the separation of the two trial types and to allow for the investigation of interaction effects between response speeds and reward. For the choice task, the AuC in the function representing associations between units of efforts and requested payoffs was computed in every participant (Myerson et al., 2001). This measure corresponds to SV of effort and has been found to be correlated with need for cognition scores in a previous study (Westbrook et al., 2013).

The RBP changes were investigated separately in alpha (8-12 Hz), beta (16-24 Hz) and theta (4-7 Hz) frequency bands across all 129 electrodes using 2×3 repeated measures ANOVAs.

A two-step procedure was used to identify electrodes suitable for further analysis. To remove electrodes with spurious results showing only minimal changes in power from the baseline (e.g., <1% changes) in each frequency band, T-tests with significance thresholds of .01 were used to test whether RBP changes over each electrode were significantly different from 0. Further, to tackle the risk of a false positive error due to the large number of tests (129), P values were corrected using a permutation analysis (Maris & Oostenveld, 2007), implemented in the statcond.m program in the EEGLab package (Makeig, Debener, Onton, & Delorme, 2004), with

the electrode labels being permuted within conditions and the null distribution being a distribution with no main effects or interactions between the reward conditions or response-speeds. Electrode clusters showing statistically significant effects in both the permutation analysis and the t-tests were explored further in SPSS v. 22 (IBM Inc., USA). The Greenhouse-Geisser epsilon correction was used to tackle a violation of the sphericity assumption found in the data. The correlations between individual RTs and individual changes in RBP were calculated to test for possible covariations between behavioural and electrophysiological effects.

4.3.2 Experiment 2

4.3.2.1 Participants

17 subjects (12 females), aged 24.05 ± 3.65 (mean ± SD) were recruited. The procedure used was approved by the Research Ethics Committee of the University of Liverpool, and all participants gave fully informed written consent at the start of the experiment in accordance with the Declaration of Helsinki.

4.3.2.2 Procedure

The procedures employed in experiment 2 were identical to those used in experiment 1 except for the structure of the blocks and the trials. The participants first completed an EEG experiment; completing a sustained vigilance task, which was a modification of the vigilance task used in experiment 1 (Dinges & Powell, 1985; Massar et al., 2016). Participants then completed the same discounting task as the one employed in experiment 1.

Participants were first presented with a white fixation cross (baseline period) followed by a cue stimulus which displayed the reward value of the next target stimulus (0p, 1p, or 10p) the fixation cross was then displayed in the centre of the

screen. After 2.5 seconds the target stimulus occurred (the fixation cross would disappear for 0.5 seconds). The presentation of the baseline period and the cue stimulus was separated by uniformly distributed inter-trial intervals which ranged from 3.5 to 9 seconds and the cue stimulus was presented for 1 second (Figure 4.1B). The participants first completed a practice block of the test which lasted for 15 trials with no rewards offered. The participants' median RT was calculated during the practice block and was then recalculated separately for each reward condition following each trial in the experimental portion of the task.

Following this baseline block, participants were presented with target stimuli in groups of three, containing one trial from each reward condition (0p, 1p, and 10p). The order of trials was pseudo-randomly rearranged at the start of each set of 3 trails, meaning that the participants could not predict the order of presentation of trials and that there were an equal number of trials in each reward condition presented throughout the duration of the experiment. In the 0p condition participants were offered one point rather than a monetary reward whenever they responded to the target stimulus faster than (or as fast as) their previously calculated median RT. In two of the reward conditions participants were offered a monetary reward whenever they responded to the target stimulus faster than (or as fast as) their previously calculated median RT. Participants were offered 1p per fast response in one condition, and were offered 10p per fast response in the other. The participants were presented with 100 target stimuli for each condition, meaning that the participants were offered a total of £0, £1 or £10 across all the trials in each reward condition. During the baseline periods of the experiment, participants were instructed to look at the fixation cross presented on the monitor without making a response.

Trials were divided in half, whereby trials which participants responded faster than their median RTs were encoded as fast trials and trials where participants responded slower than their median RTs were encoded as slow trials. Behavioural measures of attention were taken as being the mean RTs for the participants in each experimental block (0p, 1p, 10p) and response speed condition (fast, slow). The average number of trials in each condition was: 0p 73.67 ± 14.62 (mean ± SD); 1p 76.76 ± 12.84 (mean ± SD); 10p 74.95 ± 11.53 (mean ± SD). The average number of trials accepted did not differ across conditions ($p > 0.05$). Fewer trials were removed from the EEG analysis in this experiment compared to experiment 1 due to overall cleaner data.

4.3.2.3 Event-related desynchronization analysis

ERD in alpha, beta and theta bands was computed at every electrode by first calculating the absolute band-power value from 1-s time epochs shifted in 100-ms steps across a 9-s trial window. The trial time window ranged from 2 s before and 7 s after the onset of the cue signalling the amount of reward. The power spectral densities in every one of the 81time-bins were computed using the Welch method. Each data epoch was smoothed using a Hanning window. The epoch ranging from -1.5 to -0.5 s was used to evaluate rest amplitudes of cortical oscillations and this value was used to compute ERD at every time point across the trial according to the ERD transform (Equation 1). ERD values in the time epoch ranging from 2 to 3 s after the cue onset and immediately preceding the disappearance of the fixation cross were averaged for further statistical analysis.

4.3.2.4 Statistical analysis

The differences in the median RTs across three blocks and two speed conditions of the vigilance task were compared using a 2×3 repeated measures ANOVA with three levels of reward (0p, 1p and 10p) and two levels of response-speed (fast and slow). For the choice task, each participant's indifference point was calculated for each effort block (5, 10, 15, 20, 25, 30 minutes).

ERD was investigated in theta (4-7 Hz), alpha (8-12 Hz) and beta (16-24 Hz) frequency bands across all 129 electrodes using 2×3 repeated measures ANOVA. To tackle the risk of a false positive error due to the large number of tests the P values were corrected using a permutation analysis (Maris & Oostenveld, 2007), implemented in the *statcond.m* program in the EEGLab package (Makeig, Debener, et al., 2004). To prevent multiple comparisons from creating false effects electrode clusters were selected using a permutation analysis with 5000 permutations. Electrodes with statistically significant main effects or interactions were selected for further analysis. T-tests with significance thresholds of 0.001 were used to test whether ERD over each electrode was significantly different from 0. Only electrodes which passed significance thresholds in both tests were selected for subsequent analysis. The combined statistical and amplitude threshold ensured that results were extracted only from electrodes showing task-related responses.

Electrode clusters showing a statistically significant effects in both the permutation and t-test analyses were explored further in SPSS v. 22 (IBM Inc., USA). Greenhouse-Geisser epsilon correction was used to tackle the violation of the sphericity assumption due to more than two levels in the independent variable.

To test possible covariations between band power, RT changes, and individual SVs, difference variables were created. These were defined as the mean difference

between fast and slow trials for each participant, which were calculated by subtracting fast trial RTs and RBP from slow trial RTs and RBP power. The RBP and RT difference variables were correlated with each other and individual AuC of SVs using bivariate correlations.

4.4 Results

4.4.1 Experiment 1

4.4.1.1 Vigilance task

Differences in median RTs across the three reward conditions (0p, 1p, 10p), and across fast and slow trials were analysed using a 2×3 repeated measures ANOVA. A statistically significant main effect of reward was found ($F(2,56) = 6.75$, $p = .003$, $\eta p^2 = .19$) with a significant negative linear trend ($p = .001$). This was found to be the result of a difference between the 10p reward block and both the 1p ($p = .047$) and the 0p reward blocks ($p = .001$). Median RTs in slow and fast trials in each reward category are shown in Figure 4.2A.

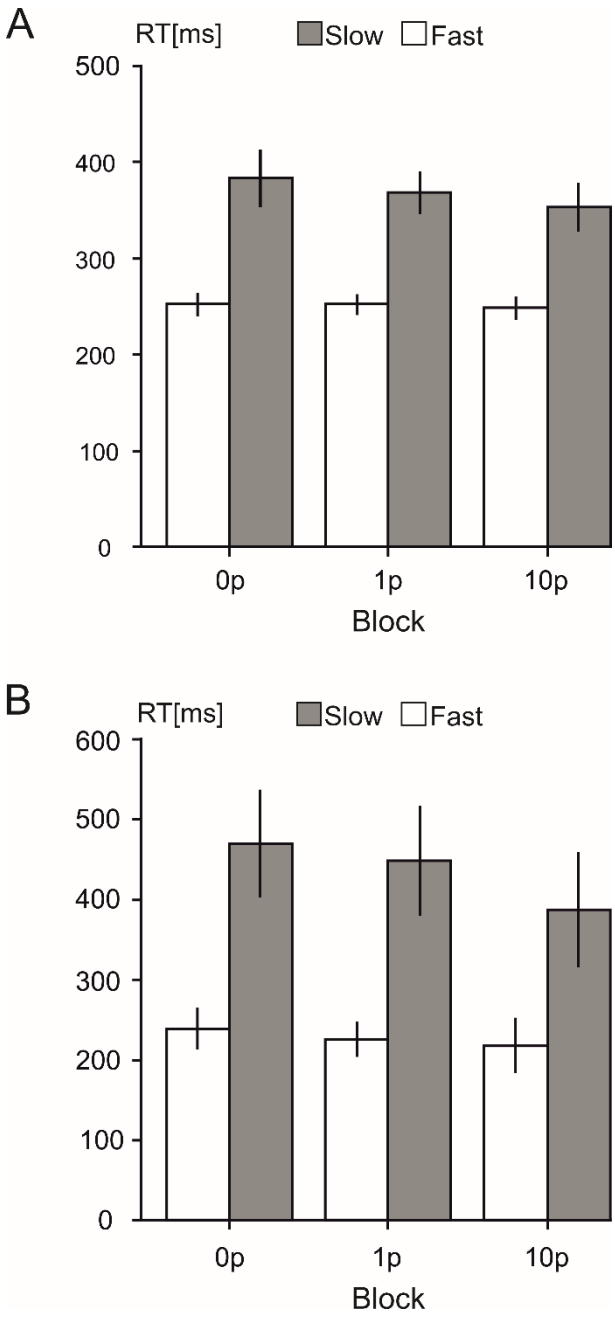


Figure 4.2. A bar chart to show the mean RTs in each reward condition (0p, 1p, 10p) in slow (grey) and fast (white) trials in experiment 1 (A) and experiment 2 (B). Error bars represent the standard errors of the mean.

A statistically significant interaction between reward and response-speed was also found ($F(2,56) = 5.03$, $p = .012$, $\eta p^2 = .15$). A test of simple effects showed that this interaction was due to an effect of reward on RTs for slow trials only ($F(2,46) = 7.15$, $p = .003$) with a statistically significant negative linear trend ($p = .002$). The main effect was found to be the result of a difference between the 10p reward block and both

the 0p (p = .001) reward block. No statistically significant effect of reward was found for fast responses.

RT difference variables were correlated with the value of effort evaluated as AuC in individual COGED graphs representing amount of money to be paid for each of the six task durations, with no statistically significant correlation being found between RT changes and individual SVs of effort (see Figure 4.3B).

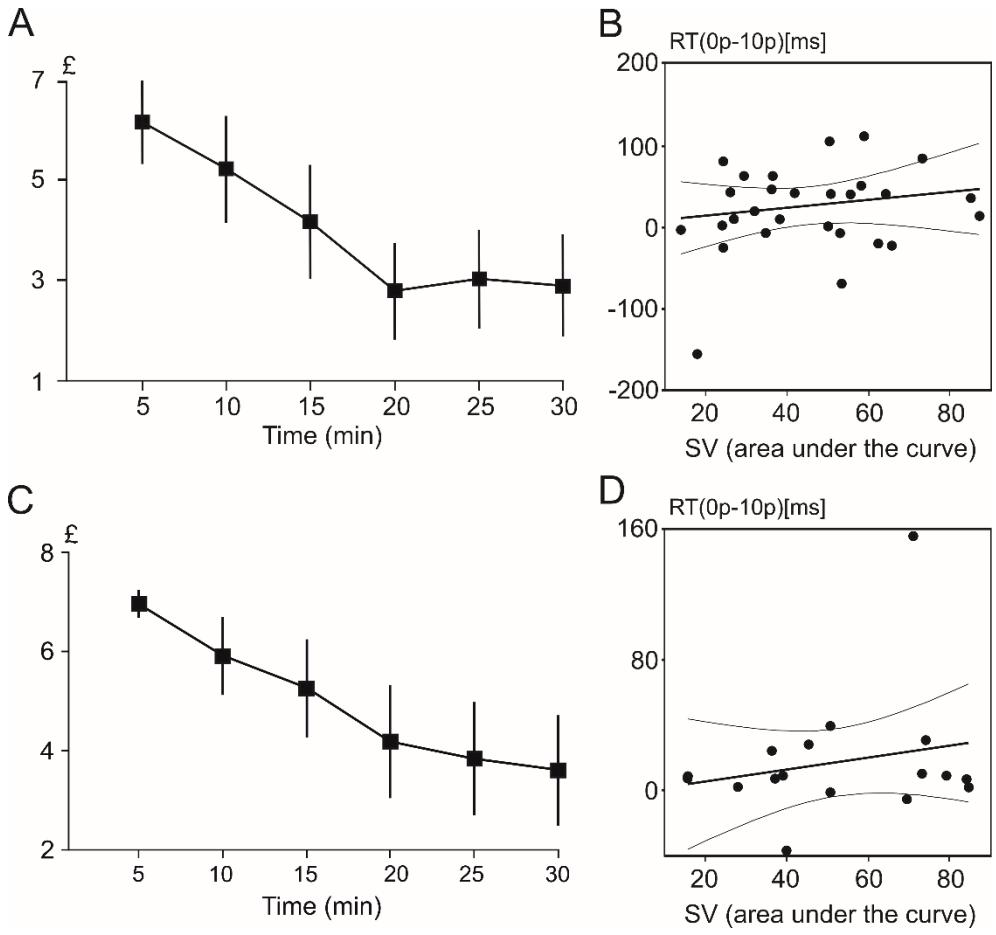


Figure 4.3. A line graph to show the discounting curve in the choice task, with the mean subjective value shown for each block in the task (5, 10, 15, 20, 25, 30 minutes). A discounting curve is shown for both (A) experiment 1 and for experiment 2 (C). Error bars represent standard errors of the mean. And scatterplots to show the correlation between the area under the curve of SVs in the discounting task and the median RTs difference between high-reward and no reward conditions (0p-10p) for experiment 1 (B) and experiment 2 (D)

4.4.1.2 Discounting task

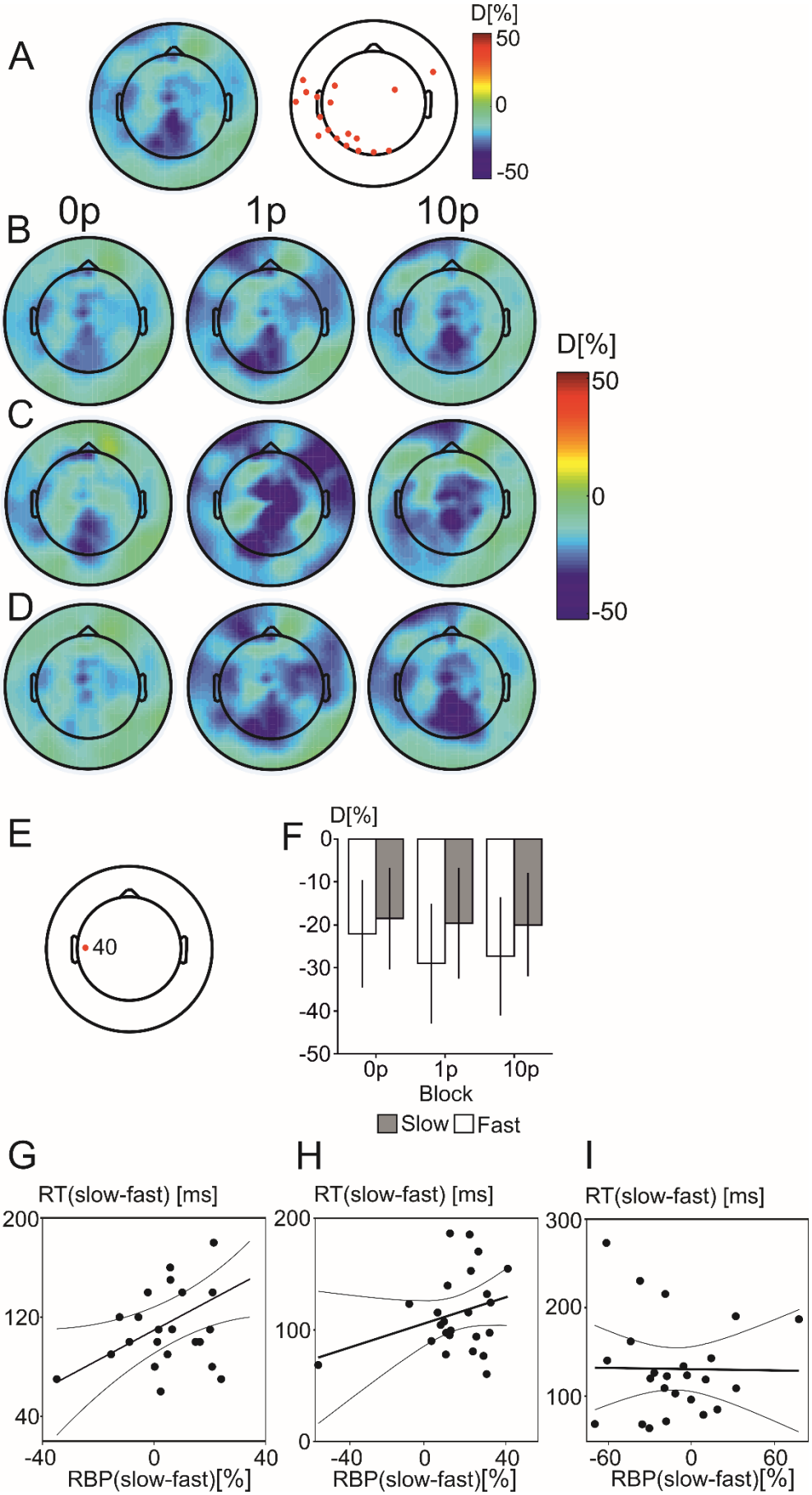
A linear regression analysis was used to compare the change in SV for each effort condition (5, 10, 15, 20, 25 & 30 minutes). The mean discounting values across offered 5-30 min task durations are shown in Figure 4.3A. There was a statistically significant exponential relationship between the levels of effort and SVs ($F(1 , 172) = 32.87$, $p < .001$, $\boldsymbol{R^2} = .17$). The regression model showed a negative exponential regression with an equation of:

$$Y = 6 \times \exp(-0.041 \times X) + \varepsilon,$$

where Y is the SV, X is the effort level, and ε is an error element.

4.4.1.3 Alpha-band changes

Figure 4.4A shows the grand average topographic maps of RBP over all trials (left), as well as the electrodes found to be different from 0 (right). Electrodes responding with amplitude changes in the alpha band included the posterior parietal and occipital cluster of electrodes, the left central-temporal cluster, and two electrodes over the right frontal and prefrontal region of the scalp. The grand average topographic maps of RBP in each of the three reward conditions are shown for slow (Figure 4.4B) and fast (Figure 4.4C) trials, as well as across all trials (Figure 4.4D).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120
40
-40
0
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RBP(slow-fast)[%]
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100
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-40
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RBP(slow-fast)[%]
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RT(slow-fast) [ms]
300
200
100
-60
0
60
RBP(slow-fast)[%]

Figure 4.4. The RBP changes in alpha band in experiment 1. (A) A grand average topographic map of alpha-RBP averaged across all conditions and subjects. (B) An overhead view of electrodes showing statistically significant changes in alpha band across all conditions. (C) Grand average topographic maps of alpha-RBP in 0p, 1p and 10p conditions during trials with slow RTs. (D) Grand average topographic maps of RBP in three reward conditions in fast RT trials. (E) Grand average topographic maps of alpha RBP in three reward conditions across all trials and the location of electrode 40 showing an interaction between reward values and speed of motor response. (F) The mean values of alpha RBP in slow (grey rectangles) and fast (white rectangles) in three reward conditions ate electrode 40. The error bars represent standard errors of the mean. Scatter plot and linear regression lines representing correlation between the difference alpha RBP (slow-fast trials) and the difference RT (slow-fast trials) at electrode 40 in 10p condition (G), the 1p condition (H), and the 0p condition (I).

The topographic maps show widespread increases in alpha RBP, with larger RBP increases preceding fast compared to slow trials over left-central region of the scalp. To investigate RBP changes over the left-central electrode 40 a 2×3 repeated measures ANOVA was conducted, with 3 levels of reward (0p, 1p and 10p) and 2 levels of response-speed (fast and slow). A significant main effect of response-speed was found ($F(1,23) = 4.37$, $p = .048$), where fast responses were found to elicit significantly stronger synchronisation compared to slow responses. Electrode location is shown in Figure 4.4E and RBP values for electrode 40 are shown in Figure 4.4F.

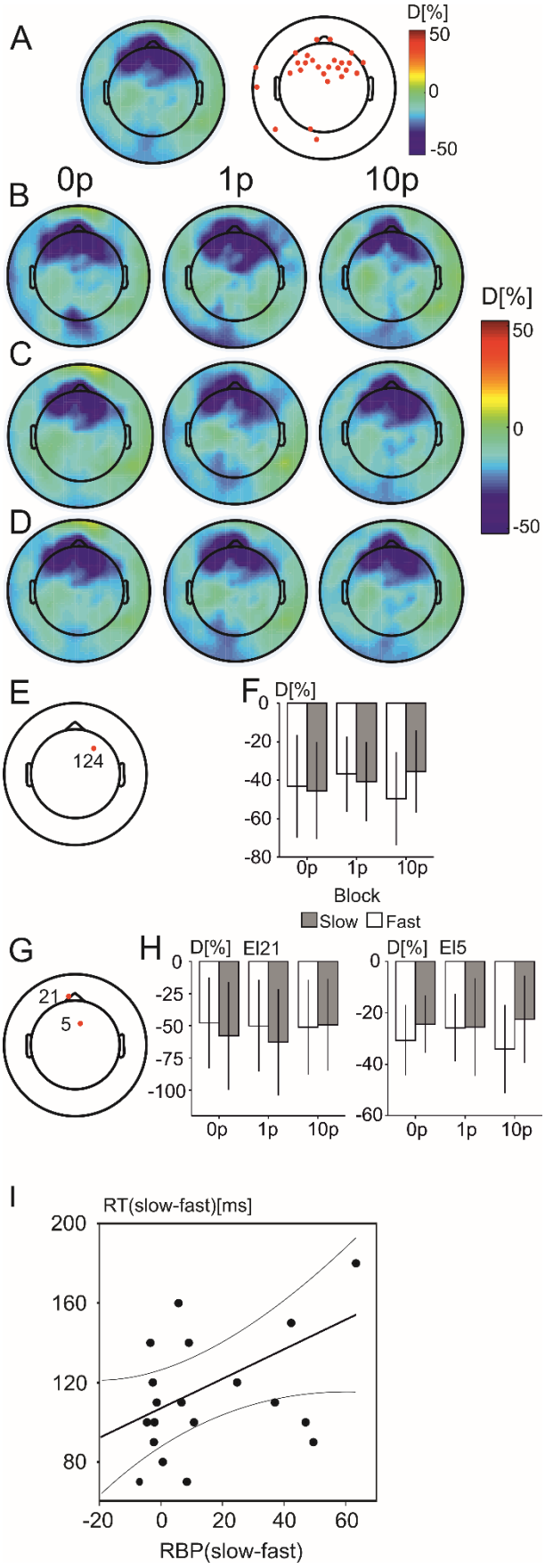
In order to assess the relationship between RBP changes and RTs, difference variables were created. These were defined as the mean difference between fast and slow trials for each participant, being calculated by subtracting fast trial RTs and RBP from slow trial RTs and RBP power. There was a significant positive correlation between alpha RBP and RT difference variables in the 10p reward block ($r(24) = .42$, $p = .015$), showing that participants with stronger synchronisation in fast relative to slow trials had shorter RTs in fast relative to slow trials. However, no significant correlations were found between the same RT and RBP difference variables created in

either the 0p ($r(24 = -.015, p = .95)$, or 1p ($r(24 = .29, p = .15)$) reward blocks. Results of these correlations are shown in Figure 4.4G-I.

The changes in alpha RBP were also correlated with the value of effort evaluated as AuC in individual COGED graphs representing amount of money to be paid for each of the six task durations. However, no statistically significant correlation was found between alpha-band power changes and individual SVs of effort acquired in COGED task.

4.4.1.4 Beta-band changes

Figure 4.5A (right panel) shows the grand average topographic maps of beta RBP over all trials (left), showing strong increases in RBP over frontal regions of the scalp at electrodes surpassing a combined statistical and amplitude threshold highlighted with red circles (left panel). The grand average topographic maps of relative band power in each of the three reward conditions are shown for slow (Figure 4.5B) and fast (Figure 4.5C) trials as well as across all trials (Figure 4.5D).


A
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F
0
D[%]
-20
-40
-60
-80
0p
1p
10p
Block
Slow
Fast
G
21
5
H
0
-25
-50
-75
-100
D[%] EI21
0
-20
-40
-60
D[%] EI5
0p
1p
10p
I
RT(slow-fast)[ms]
200
160
120
80
-20
0
20
40
60
RBP(slow-fast)

Figure 4.5. The relative band power changes in beta band in Experiment 1. A. Grand average topographic map of beta RBP across all conditions and subjects. B. An overhead view of electrodes showing statistically significant changes in beta band across all conditions. C. Grand average topographic maps of beta RBP in 0p, 1p and 10p conditions during trials with slow RT. D. Grand average topographic maps of beta RBP in three reward conditions in fast RT trials. E. Grand average topographic maps of beta RBP in three reward conditions across both slow and fast RT trials. E. Location of electrode 124 showing an interaction between reward values and speed of motor response. F. The mean values of beta RBP in slow (grey rectangles) and fast (white rectangles) in three reward conditions at electrode 124. The error bars stand for standard errors of the mean. G. Locations of electrodes 121 and 5 showing a statistically significant main effect of response speed. H. The left-hand panel shows mean beta RBP at electrodes 121 and 5 in three reward conditions for slow (grey rectangles) and fast (white rectangles) trials. I. The scatter plot and linear regression line with 95% confidence interval lines depicting association between differences in RT (slow-fast trials) and differences beta-band RBP (slow-fast trials) .

A statistically significant interaction between reward and response-speed was found over the right-frontal region of the scalp (electrode 124) ($F(2,46) = 4.51$, $p = .016$). The interaction was found to be due to an effect of response-speed in the 10p reward block ($F(1,23) = 9.37$, $p = .006$), where fast responses were found to elicit statistically significantly more beta-band synchronisation compared to slow responses. Electrode location is shown in Figure 4.5E and mean values of beta-band RBP in all conditions are shown in Figure 4.5F.

A statistically significant main effect of response-speed was found over a frontal electrode (electrode 21) ($F(1,23) = 5.64$, $p = .026$), where fast responses were found to elicit significantly weaker beta band synchronisation compared to slow-responses. In contrast, electrode 5, located in the midline fronto-central area of the scalp (Figure 4.5G), showed a stronger beta-band power increase in fast compared to slow responses ($F(1,23) = 9.23$, $p = .006$) (Figure 4.5H).

To evaluate the relationship between RTs and RBP over right-frontal regions (electrode 124) a difference variable was calculated in both RTs and RBP values representing the differences between fast and slow trials in the 10p reward block only,

being calculated by subtracting fast trial RBP and RTs from slow trial RBP and RTs. The Pearson product-moment correlation showed a statistically significant positive relationship between the difference values computed for RTs and RBP over electrode 124 ($r(24) = .44$, $p = .033$) (Figure 4.5I). This shows that participants with a stronger increase in beta-band power in fast trials compared to slow trials in the 10p reward bock also had a greater difference in RTs between slow and fast trials in this block. No significant correlation was found between RBP changes in the beta band and individual discounting results.

Data was also analysed in the theta frequency band, however, no electrodes were found to pass both significance thresholds in this frequency range.

4.4.1.5 Absolute band power changes

In order to confirm that the effects found within the alpha- and beta-bands were not the results of changes in baseline power, the absolute power of the baseline conditions was compared over relevant electrodes in the alpha- and beta-bands. No significant differences in baseline were found across reward conditions for any of the relevant electrodes ($p > .05$) in either frequency band, confirming that the results of experiment 1 were not the result of variations within the baseline power.

4.4.2 Discussion

The results of experiment 1 show that the presence of monetary incentives shortened RTs, and increased and focused cortical beta oscillations over frontal scalp regions in the period just preceding a motor response. Individual values of subjective effort, however, were not associated with band-power increases in either the alpha or beta frequency bands. Thus, we were unable to replicate the correlation of $r = 0.31$ between the value of effort and the shortening of RTs found in previous research

(Massar et al., 2016). However, the order of the three reward blocks was randomised in the present study, whereas in previous research the no reward block was always presented first. This procedural difference may explain the lack of a statistically significant correlation between the individual value of effort and performance.

The effects of response-speed were seen as modulations of amplitude increases in both alpha- and beta-band power in the 1-s epoch preceding the motor response, compared to the baseline. In the alpha band, a stronger increase in oscillatory power was observed in fast compared to slow trials over a left-central electrode. This effect was significantly correlated with the individual differences between fast and slow mean RTs. An effect of reward was present only in the beta band, as a stronger synchronisation of beta-band oscillations prior to fast compared to slow responses in 10p condition but not in 0p or 1p conditions. Individuals with the largest differences between slow and fast RTs also showed the strongest increase in beta-band power at the frontal electrode.

Amplitude increases in the alpha-band over central regions have traditionally been associated with motor inhibition (Adam Fry et al., 2016; Jensen et al., 2005; Gert Pfurtscheller et al., 1996; Salmelin & Hari, 1994). This is thought to be due to the absence of excitatory impulses from lower brain centres (e.g., the reticular formation) (Bonvallet & Newman-Taylor, 1967; Steriade & Demetrescu, 1962; Zaaimi, Dean, & Baker, 2018) and due to the synchronised firing of GABAergic neurons (Faust, Assous, Tepper, & Koós, 2016; Jensen et al., 2005; Klimesch et al., 2007; Tritsch, Granger, & Sabatini, 2016).

The strength and presence of reward significantly modulated increases in oscillatory power in the beta band over frontal electrodes. Increased amplitude of beta oscillations likely signifies a short-term cortical inhibition allowing participants to

withhold motor responses more effectively in the 10p reward block. This interpretation is supported by findings of activations in the right frontal cortex during stop-signal and Go/No Go tasks (Aron & Poldrack, 2006; Matzke, Verbruggen, & Logan, 2018; Wessel & Aron, 2015), and of increased beta-band synchronisation over frontal electrodes during motor inhibition (Alegre et al., 2006; Fonken et al., 2016; Swann et al., 2009; Wagner et al., 2018; Wessel & Aron, 2013). The pattern of cortical oscillations in experiment 1 matched the inhibitory processes posited by the horse-race model of motor actions (Band et al., 2003; Logan, 1994; Logan & Cowan, 1984), showing that active inhibition was required during motor preparation and that this was modulated by reward and response speed.

Both the alpha- and beta-band results suggest that higher rewards and faster response speeds were associated with increased motor inhibition in the time window preceding movement. This relates to the experimental design, where the target was not cued, so motor activation was required to be maintained throughout each block. The increased inhibition found may relate to higher engagement with the task or be due to a faster motor response, and the correlation found between RTs and RBP in the 10p reward block support this explanation.

4.4.3 Experiment 2

4.4.3.1 Vigilance task

Differences in median RTs in response to the target stimulus were assessed across the 3 reward conditions (0p, 1p & 10p) in both fast and slow trials using a 2×3 repeated measures ANOVA. A significant main effect of reward was found ($F(2,32) = 12.58$, $p = .001$, $\boldsymbol{\eta p^2} = .44$), with a significant negative linear trend ($p = .002$). This main effect was found to be the result of significant differences between the 10p reward condition and both the 1p ($p = .003$) and the 0p ($p = .002$) reward conditions.

The mean values of RTs in each reward and response-speed conditions are shown in Figure 4.2B.

A significant interaction was also found between reward and response-speed ($F(1,32) = 10.80$, $p = .002$, $\boldsymbol{\eta p^2} = .40$) and, in order to investigate this interaction one-way repeated measures ANOVAs assessed the effect of reward on RTs during fast and slow trials separately. The interaction was related to the statistically significant modulation of RTs during slow trials only ($F(2,32) = 12.84$, $p = .001$, $\boldsymbol{\eta p^2} = .45$) with a significant negative linear trend ($p = .001$). Further analysis of post-hoc effects revealed a significant difference between the 10p reward condition and both the 1p ($p = .001$) and 0p ($p = .001$) reward conditions. No statistically significant simple effect of reward on RTs were found in fast trials.

A difference variable representing the high reward RTs subtracted from low reward RTs (10p-0p) correlated with the AuC in individual COGED graphs. However, no statistically significant correlation was found between RT changes and individual SVs of effort acquired in COGED task (see Figure 4.3D).

4.4.3.2 Discounting task

A linear regression analysis was conducted to compare the change in SV for each block during the discounting task (5, 10, 15, 20, 25, 30 minutes). There was a significant exponential relationship between the levels of effort and SVs ($F(5 , 15) = 6.66$, $p < .002$, $\boldsymbol{R^2} = .69$) (Figure 4.3C). The regression model showed a negative exponential regression with an equation of:

$$Y = 7.36X — 0.14 + \varepsilon,$$

where Y is the SV, X is the effort level, and ε is an error element.

4.4.3.3 ERD patterns across trials.

Figs. 6A-C shows the time courses and topographic maps of alpha-, beta- and theta-ERD/ERS across trials, respectively. Oscillations during the cue interval (0.5 s after cue onset) were featured by an ERD over occipital electrodes in the alpha band (Figure 4.6A). This is consistent with the presence of attentional and visual processing of a reward cue. During the period of motor readiness (2-2.5 s after cue onset), alpha-ERD was prominent in left (contralateral) parietal, and central electrodes. After the cue disappeared and during the time of motor response, alpha-ERD was distributed bilaterally in parietal, and central electrodes.

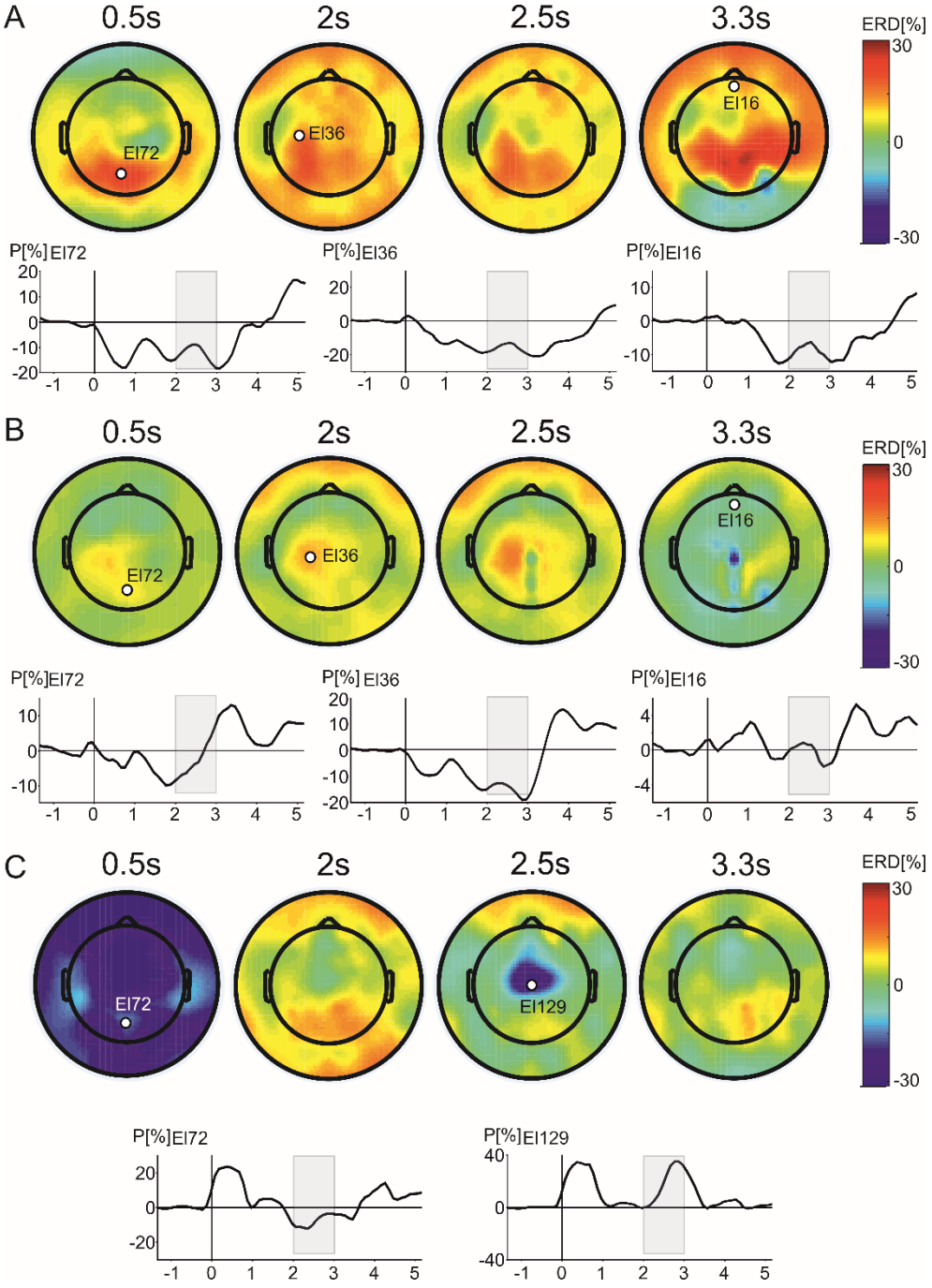

Figure 4.6. Topographic maps of alpha (A), beta (B) and theta (C) ERD at four time points: during presentation of visual cue (0.5 s), early period of anticipation of motor response (2 s), late period of motor response anticipation (2.5 s) and during motor response (3.3 s). In each section (A-C), ERDs at selected electrodes are also shown. The grey rectangles covering the interval from 2 s to 3 s represent the epoch of interest preceding the motor response.

In the beta band (Figure 4.6B), a comparatively weak ERD appeared in the contralateral central electrodes during the period of motor readiness preceding the

disappearance of the fixation cross. A beta-ERS was seen at the vertex electrode during motor preparation (2.5 s after cue onset). This increased during the motor response period (3.3 s after cue onset).

Finally, in the theta band (Figure 4.6C), activation during the cue interval (0.5 s after cue onset) was confounded by the presence of the phase-locked evoked response causing an increase of theta power over the whole scalp. The period of motor readiness (2.5 s after cue onset) was featured with a theta-ERS at central and precentral midline electrodes.

4.4.3.4 Alpha-band ERD

The grand average topographic maps showing alpha-band ERD for all trials as well as the electrodes found to be significantly different from zero are shown in Figure 4.7A. Two clusters of electrodes, one in bilateral parietal and central electrodes and another in frontal electrodes, showed alpha-ERD surpassing both the combined amplitude and statistical thresholds.

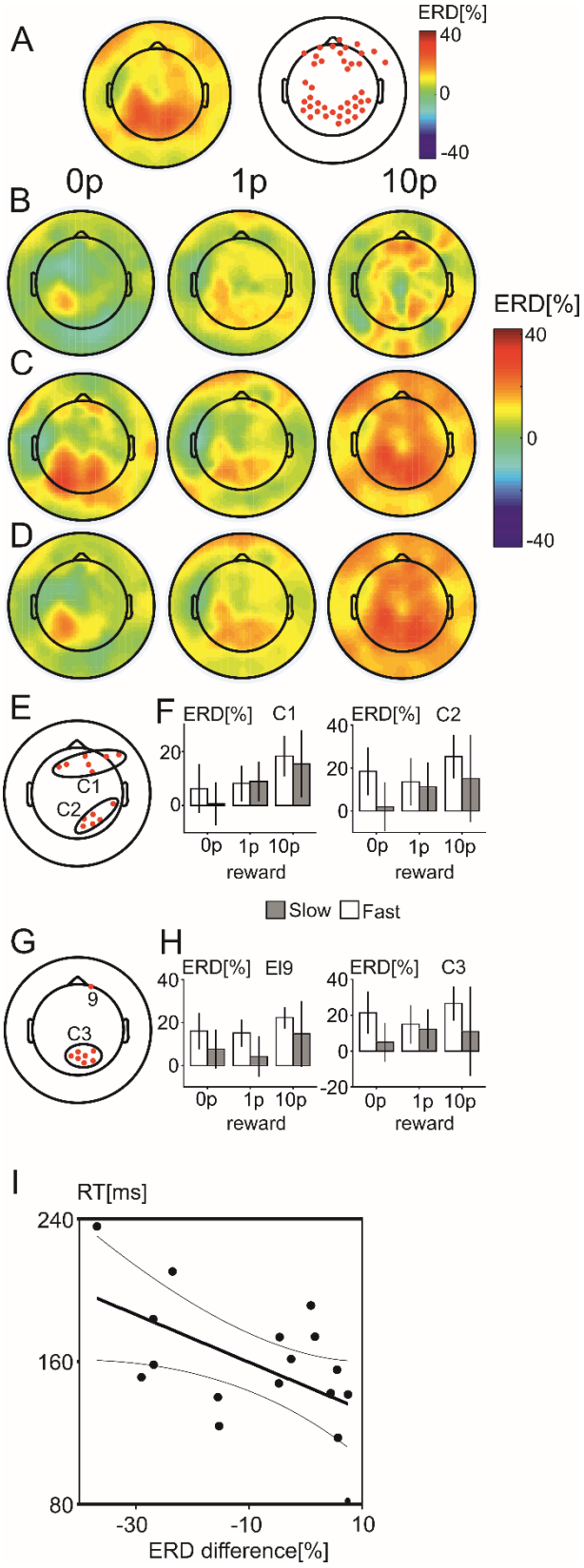

Figure 4.7. Alpha-band ERD during anticipation of motor response A. Topographic map of alpha-band ERD across all conditions and trials (left), and electrodes showing a prominent alpha-band ERD across all conditions (right). B. Topographic maps of alpha-band ERD in three reward conditions during slow ER trials. C. Topographic maps in each of three reward conditions in fast RT trials. D. Topographic maps

showing the mean alpha-band ERD across all trials. E. Location of electrodes in two clusters manifesting statistically significant effect of reward. F. Bar charts showing mean alpha-band ERD each of three reward conditions in slow (grey rectangles) and fast (white rectangles) RT trials. Error bars represent standard error of the mean. G. Locations of electrodes displaying a statistically significant main effect of speed of motor response. I. A scatterplot and the linear regression line with 95% confidence lines illustrating the statistically significant correlation between alpha-band ERD differences (slow-fast RT trials) and RT differences in electrode 9.

Topographic maps showing ERD in each of the three reward conditions are shown In Figure 4.7B for slow, and Figure 4.7C for fast trials, and in Figure 4.7D for all trials irrespective of the speed of the motor response.

To investigate the effects of response-speed and reward on ERD values 2×3 repeated measures ANOVAs were computed to assess the significant main effects and interactions of response-speed (fast & slow) and reward (0p, 1p, 10p) on ERD recorded by electrodes which passed the combined statistical and amplitude thresholds. This ensured that only electrodes showing a robust ERD across conditions were analysed.

Statistically significant main effects of reward were found in both frontal and occipital regions of the scalp. Over frontal electrodes (cluster 1) ERD grew significantly stronger as reward increased ($F(2,32) = 7.95$, $p = .003$, $\boldsymbol{\eta p^2} = .44$), and a statistically significant positive linear trend was found ($p = .005$). The observed main-effect of reward was due to a difference between ERD in 10p reward trials and both 0p ($p = .005$) and 1p reward trials ($p = 0.008$). There was also a statistically significant effect of reward on ERD found over right-parietal regions (cluster 2) ($F(2,32) = 4.31$, $p = .022$, $\boldsymbol{\eta p^2} = .31$), with a statistically significant linear trend ($p = .017$). This effect was found to be the result of a difference between ERD calculated for 10p trials and for 0p trials ($p = .017$). Electrodes with a main effect of reward are shown in Figure 4.7E, and results for both cluster 1 and cluster 2 are shown in Figure 4.7F.

Significant main effects of response-speed were also found over frontal and occipital electrodes, where fast trials were found to elicit significantly stronger ERD when compared to slow trials. There was significantly stronger ERD found over electrode 9 (frontal) during fast trials compared to slow trials ($F(1,16) = 6.21$, $p = .024$, $\eta p^2 = .28$), and stronger ERD over cluster 3 (occipital) during fast compared to slow trials ($F(1,16) = 5.21$, p .037, $\eta p^2 = .25$). Electrodes with a significant main effect of response-speed are shown in Figure 4.7G and ERD results for electrode 9 and cluster 3 are shown in Figure 4.7H.

A difference variable was created to by subtracting fast from slow trials for both individual ERD values over electrode 9 and individual RTs. A significant negative correlation was found between these two difference variables ($r(17) = -.55$, $p = .021$), showing that stronger differences in ERD between fast and slow trials were associated with larger differences in RTs between these trials (Figure 4.7I).

Difference variables were also created to calculate the mean difference between the ERD found during 10p reward trials and both 1p and 0p reward trials in cluster 1, and to calculate the mean difference in the participant's indifference points taken from the COGED task during 5 min and 30 min effort conditions. There was, however, no statistically significant correlation between the SV of effort, evaluated as AuC of individual COGED functions, and alpha-band ERD.

4.4.3.5 Beta-band ERD

The grand average topographic map for all trials and the distribution of electrodes showing ERD significantly different from zero are shown in Figure 4.8A. The electrodes with a strong beta-ERD across conditions were located primarily in the left, right-central and parietal electrodes. The grand average topographic maps in each

of the three reward conditions are shown for slow trials in Figure 4.8B, for fast trials in Figure 4.8C, and for all trials in Figure 4.8D.

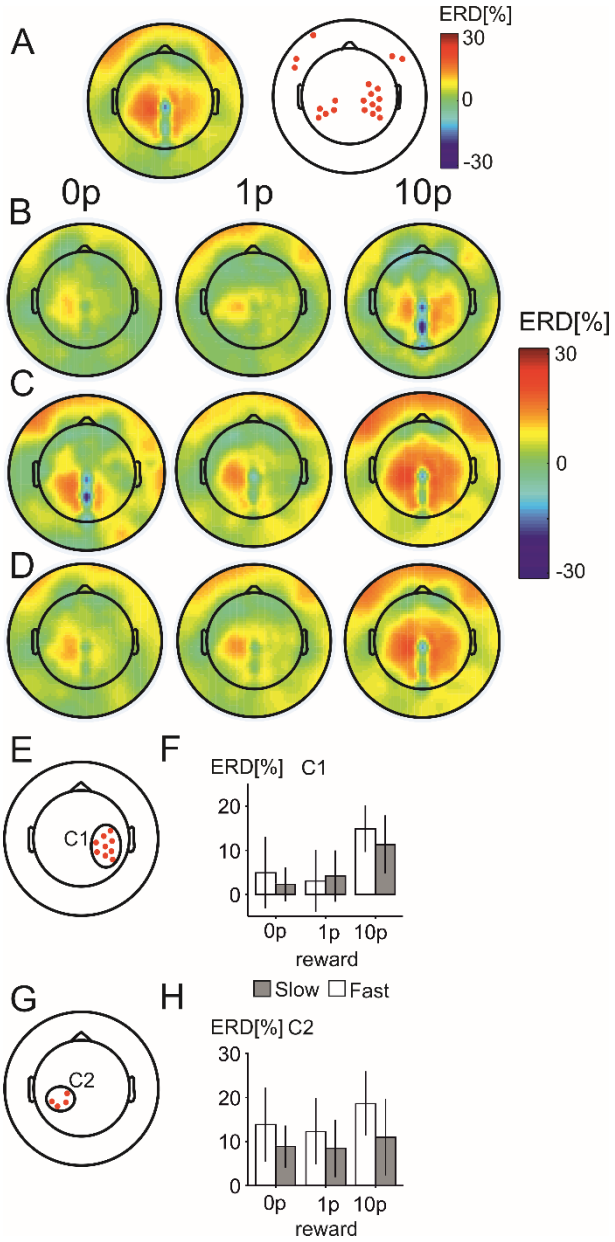

Figure 4.8. Topographic maps and statistically significant effects in beta-band ERD. A. Grand average beta-band ERD across all trials and subjects (left panel) and locations of electrode clusters manifesting a statistically significant beta-band ERD (right panel). B. Topographic maps of beta-band ERD in three reward conditions (0p, 1p and 10p) in slow RT trials. C. Topographic maps of beta-band ERD in fast RT trials. D. Topographic maps of beta-band ERD in three reward conditions averaged across fast and slow trials. E. Location of the electrode cluster, labelled C1, showing a statistically significant effect of reward. F. Mean values of beta-band ERD in the cluster shown in (F) in three reward conditions in slow (grey rectangles) and fast (white rectangles). The error bars stand for standard errors of the mean. (G.) The location of electrode cluster, labelled C2, showing a statistically significant effect of speed of

motor response. (H.) Mean values of beta-band ERD in three reward conditions in slow (grey rectangles) and fast (white rectangles) RT trials.

ERD in the beta band featured a comparatively weak effect in the contralateral central and parietal electrodes in the 0p and 1p conditions compared to the 10p condition. Beta-ERD was also pronounced over ipsilateral central electrodes, however this effect was only found in the 10p condition. ERS can also be seen over central regions (electrodes Cz to Oz), an effect consistent with the 'surround ERS' (Piotr Suffczynski, Kalitzin, Pfurtscheller, & Da Silva, 2001) found around areas showing ERD in previous studies (Doyle et al., 2005; Christa Neuper, Wörtz, & Pfurtscheller, 2006; Pfurtscheller, 2003; Pfurtscheller, Neuper, & Krausz, 2000).

There was a significant main effect of reward in the ipsilateral (right) sensorimotor hand area (cluster 1, Figure 4.8E) ($F(2,32) = 10.14$, $p = .001$, $\eta p^2 = .58$), with a significant positive linear trend ($p = .004$) (Figure 4.8F). The main effect of reward was related to the statistically significant difference between 10p reward and both the 1p ($p < .001$) and 0p reward conditions ($p < .001$).

In the contralateral (left) cluster of electrodes (cluster 2, Figure 4.8G), beta-band ERD was significantly stronger when preceding fast trials compared to slow trials ($F(1,16) = 10.39$, $p = .005$, $\eta p^2 = .39$) (Figure 4.8H). There was no effect of reward in cluster 2 ($p > .05$).

In order to evaluate the relationship between behavioural results and beta-ERD found ipsilateral to the hand movement a difference variable was created where the mean ERD difference between 10p reward trials and both 1p and 0p reward trials was calculated. However, there was no statistically significant correlation between beta-band ERD and RT difference values. Similarly, there was no statistically significant

correlation between beta-band ERD and the SV of effort in any of the electrode clusters ($p > 0.05$).

Similar to experiment 1, there were no statistically significant effects of reward or speed of response in theta band.

4.4.4 Discussion

Reward level quickened RTs, especially in slow movements. The COGED profiles showed decreasing SVs of reward as the associated effort was increased similar to previous studies (Massar et al., 2016; Westbrook et al., 2013). However, no significant correlation was found between the SV of effort and either RTs or cortical oscillatory changes. We were, again, unable to replicate the correlation between value of effort and RTs found in Massar et al. (2016). It appears that this correlation is difficult to replicate if the order of blocks or trials with different reward levels occurs in a random order, showing independence between the individual value of effort and the way rewards effected the modulation of effort during the vigilance task.

ERD in the alpha band showed reward-related increases, with the strongest ERD in the 10p condition in two clusters of electrodes, one in the frontal and the other the parietal region of the scalp. Both regions also showed a stronger ERD prior to fast, compared to slow motor responses. In the beta-band, ERD was localised in contralateral central regions of the scalp, purportedly overlaying the sensorimotor hand areas, and was stronger preceding fast compared to slow responses. This ERD response became bilateral during the 10p reward conditions before both fast and slow trials, but not during the 0p or 1p reward conditions.

Theta-band oscillations showed fronto-central synchronisation prior to the target stimulus, a response associated with increased attention and effort (Angelidis et al., 2018; Basar-Eroglu et al., 1992; Wolfgang Klimesch, 1999; Rajan et al., 2018).

This was, however, not modulated by reward or response speed, showing that it was not related motor preparation or may have a ceiling effect.

The alpha-band ERD in posterior parietal regions is likely to refer to the activation of regions involving visual-spatial coordination localised in the posterior parietal cortex (Assmus, Marshall, Noth, Zilles, & Fink, 2005; Corbetta, Kincade, Ollinger, McAvoy, & Shulman, 2000; Ibos & Freedman, 2016; Whitlock, 2017). ERD in posterior parietal electrodes has also been observed during the preparation of shoulder movements (Stancak, Feige, Lucking, & Kristeva-Feige, 2000). This may indicate more generalised motor readiness during intense effort, which may, initially, involve larger muscle groups even if the target movement is only a hand movement. The alpha-band ERD in the prefrontal regions supports the hypothesis that this region is implicated in motor preparation, or in the activation of cortical areas involved in motor preparation (e.g., motor areas or the basal ganglia) (Aron & Poldrack, 2006). This interpretation is strengthened by the significant correlation between alpha-band ERD and individual RTs, and the present results show that these effects can be elicited by increasing performance-based rewards.

Fast compared to slow motor responses were preceded by increased beta-ERD in electrodes overlying the contralateral sensorimotor cortex, which is likely to refer to increased motor preparation during fast trials (Fry et al., 2016; Ishii et al., 2019; Rhodes, 2019; Tewarie et al., 2018; Tzagarakis et al., 2015). The effect of reward on beta-band oscillations is supported by previous research, in which voluntary movements have been shown to be preceded by ERD in bilateral sensorimotor cortical regions (Fry et al., 2016; Little, Bonaiuto, Barnes, & Bestmann, 2018; Neuper & Pfurtscheller, 2001b; Stancak & Pfurtscheller, 1996; Stancak et al., 1997). A similar effect was found by Stancak et al. (1997), where desynchronization in the beta band

manifested in the ipsilateral somatosensory region under intermediate, but not zero, external load. The results of the present study adds to the literature by showing that incentive can elicit this effect, possibly relating to a ceiling effect in the contralateral sensorimotor cortex, boosting motor readiness in the ipsilateral sensorimotor cortex under strong effort.

Overall, the results of experiment 2 show increases in cortical activation in parietal and central electrodes paralleling increases in reward and shortening of RTs. These associations between amplitude decreases of cortical oscillations, and reward and performance could relate to the heightened level of motor readiness assumed to underlie fast responses in the horse-race model of motor control (Logan & Cowan, 1984).

4.5 General discussion

The present results add weight to our current understanding of cognitive effort by showing that reward can modulate effort through the activation or inhibition of relevant cortical areas in the short epoch preceding a speeded motor response in a sustained vigilance task. However, results suggest that the cortical mechanisms employed differ widely depending on the structure of the vigilance task.

If the task was conducted as a series of speedy movements executed under the same reward level (experiment 1) a sustained motor preparation was required which lasted throughout the entire block. Optimal motor performance was likely achieved as a combination of high motor readiness and inhibition in the frontal cortex; where the inhibitory component, indexed as increases of beta-band oscillations in frontal electrodes, prevailed.

In contrast, if the experiment was conducted with the three reward conditions alternating in a pseudo-random fashion with cues signalling the reward levels at the

start of each trial (experiment 2), optimal performance could be achieved by a continuous build-up of activation in task-relevant cortical regions. This version of the sustained vigilance task allowed the cortical regions to reach a resting state after each movement because participants were certain that no motor response was required in the time period preceding the reward cue stimulus. Thus, to achieve a fast response, the activation in the sensorimotor, premotor and other cortical areas would need to increase from a state of low activation and reach a state of high activation within the span of two to three seconds. This process of building activation in the sensorimotor cortex did not require a parallel inhibition like in experiment 1, in which short RTs would be achieved if the sensorimotor cortex was continuously active.

A novel result was found in experiment 2, showing that when participants are offered sufficient reward (10p) activations are found bilaterally in the sensorimotor cortex. This indicates that strong enough motivation can lead to motor preparation being employed in both the contralateral and ipsilateral motor areas, and adds to previous research finding bilateral sensorimotor ERD during movement (Fry et al., 2016; Little et al., 2018; Neuper & Pfurtscheller, 2001b; Stancak & Pfurtscheller, 1996; Stancak et al., 1997). This suggests that this effect occurs due to activation from the contralateral region 'spilling-out' into, or employing resources from the ipsilateral region. Movement-related ERD has been found to be stronger and more bilateral in elderly compared to younger participants (Derambure et al., 1993; Vallesi, McIntosh, Kovacevic, Chan, & Stuss, 2010). The present results suggest this effect occurs because elderly participants have to make more of an effort to make the same movement compared to younger participants.

Taken together, the cortical oscillatory patterns seen in experiment 1 and 2 act according to the horse-race model of motor control (Logan, Cowan, & Davis, 1984).

The horse-race model assumes two antagonised processes, one generating a response to the primary task and the other inhibiting it. In experiment 1, the increases of beta-band power in frontal cortical regions in the high-reward condition could be the manifestation of the inhibition process. This would be expected to be found in the frontal cortex, which has been shown to mediate motor inhibition in stop-signal and go/no-go tasks (Aron, 2007; Sakagami et al., 2006; Wessel & Aron, 2015), perhaps via the subthalamic nucleus in the basal ganglia (Aron, 2007; Eagle & Robbins, 2003; Fischer et al., 2017). This may also relate to an optimization of dopamine levels in the prefrontal cortex, which has been associated with increased cognitive stability (Cools, 2016; Cools, Clark, Owen, & Robbins, 2002; Durstewitz, Seamans, & Sejnowski, 2000; Sharp, Foerde, Daw, & Shohamy, 2016), and may, therefore, be required in experiment 1 due to the block design. In experiment 2, the time courses of ERD in the alpha and beta band showed a build-up during the interval preceding the motor response (Figure 4.6A/B). This was motivationally relevant and occurred in areas associated with motor preparation and visuo-spatial attention (Fry et al., 2016; Ibos & Freedman, 2016; Tewarie et al., 2018; Whitlock, 2017), possibly showing the excitatory components posited by the horse-race model of motor actions.

The individual value of effort did not correlate with either amplitude increases in beta-band oscillations in experiment 1, or beta-band decreases in experiment 2. It is likely that individual values of effort are implemented during the decision about whether to engage into an effortful cognitive task, but not during an ongoing task. Expected reward level, on the other hand, acted as a modifier of effort by imposing a top-down modulation of the inhibitory and excitatory processes to boost performance. Our results also add weight to the idea of cognitive effort being the result of cognitive control (Kurzban, 2016; Shenhav et al., 2013b), a signal which modulates the task-

appropriate inhibition and excitation of cortical response. This ties into to the horse-race model of motor control, and shows that these responses can be modulated by monetary incentives.

4.6 Conclusion

Decreasing RTs as the result of the presence and magnitude of reward was associated with cortical oscillatory changes in both experiment 1 and experiment 2. Experiment 1 showed a modulation of cortical inhibition in frontal, prefrontal, and central regions, suggesting that reward modulated RTs through the holding and release of inhibition. Experiment 2 showed a modulation of cortical activation over motor, frontal, and posterior-parietal regions, suggesting that reward modulated RTs through changes in motor preparation and visuo-spatial co-ordination in this modified task. Taken together, these results show the dual-processes proposed by the horse-race model of motor action, showing that both inhibition and preparation can be manipulated using performance-based rewards, and ties these to the hypothesis that cognitive effort results from top-down cognitive control, and can be encouraged with monetary incentives.

Chapter 5

Changes in anticipatory ERD during an effortful task when incentivised with a gain or loss.

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This experiment investigated the cortical oscillatory changes in response to graded losses and gains during a sustained vigilance task. This paper was submitted to the International Journal of Psychophysiology.
The format of the text has been modified to match the style of this thesis.
The roles of the co-authors are summarised below:
I designed the study in collaboration with Andrej Stancak and collected the data. Danielle Hewitt, Jessica Henderson, Alice Newton-Fenner, Hannah Roberts, and John Tyson-Carr assisted with the collection of data and contributed useful comments whilst preparing the manuscript for publication. Andrej Stancak, and Timo Giesbrecht contributed to the experimental design as well as the large-scale planning of this project. Andrej Stancak and Timo Giesbrecht secured funding for project.

5.1 Abstract

Losses are generally more motivating than gains. However, gains and losses have been shown to have similar effects on effortful performance. We explored how graded levels of losses and gains and subjective value of effort affected performance and preparatory motor activity in sensorimotor and frontal cortices during a sustained-vigilance reaction time (RT) task with graded positive and negative incentives.

Participants performed speeded responses while expecting a monetary reward (5 p, 10 p), avoiding a monetary loss (-5 p, -10 p), or receiving no incentive (0 p) if they responded faster than their median RT. Amplitudes of cortical alpha-, beta-, and theta-oscillations were analysed using the event-related desynchronization (ERD) method during the period of motor preparation. Subjective value (SV) of effort was evaluated using a cognitive effort discounting (COGED) task in gain and loss conditions.

RTs were significantly faster, and alpha- and beta-band ERD was significantly stronger over contralateral sensorimotor, and over frontal areas in the alpha-band, as larger incentives were offered, regardless of whether the incentives were losses or gains. There was no significant difference in the slopes of RTs or ERDs between gains and losses. Participants were willing to expend more effort when they expected losses compared to gains, but SV did not correlate with RTs or ERD during the vigilance task.

Results suggest a symmetric effect of graded losses and gains on performance and cortical activity prior to a speeded reaction time movement. Effortful performance is likely determined by instantaneous evaluation of reward magnitude and the state of sensorimotor cortex activity but not by economic value of effort.

5.2 Introduction

The neural mechanisms of cognitive effort have been researched in a number of different ways, showing how effort affects and is affected by individual traits (Cacioppo & Petty, 1982; Levin, Huneke, & Jasper, 2000), blood glucose levels (Fairclough & Houston, 2004; Gailliot & Baumeister, 2007), and dopamine transmission in the brain (Cools, 2016). A novel way of investigating this topic is by incorporating decision-making methods with neural activation and inhibition, measured through the modulation of cortical oscillations.

Our previous study (Byrne et al., 2020) used ERD methods to show how monetary incentives differentially improved cognitive effort through motor preparation and inhibition during a sustained vigilance RT task. Individual effort discounting rates (measured using a COGED procedure), however, did not correlate with either ERD or RT changes, showing a fractionation between motivation and the cognitive performance displayed during an effortful task.

A similar disconnect between performance and motivation has also been found between monetary gains and losses. Both gains and losses can be used to improve performance on a range of cognitive tasks (Botvinick & Braver, 2015; Braver et al., 2014; Krebs & Woldorff, 2017; Massar, Lim, Sasmita, & Chee, 2016; Walsh, Carmel, & Grimshaw, 2019), and losses have been found to be more motivating than gains (Baumeister, Bratslavsky, Muraven, & Tice, 1998; Krebs & Woldorff, 2017; Rozin & Royzman, 2001; Wright & Rakow, 2017). However, losses do not improve cognitive performance more than gains (Boksem, Tops, Kostermans, & De Cremer, 2008; Maruo, Schacht, Sommer, & Masaki, 2016; Seifert, Naumann, Hewig, Hagemann, & Bartussek, 2006), and may even cause a decrease in performance relative to gains (Fontanesi, Palminteri, & Lebreton, 2019; Paschke et al., 2015; Potts, 2011). For

example Carsten, Hoofs, Boehler, and Krebs (2018), found that participant's RTs during a Stroop task were significantly slower when they were threatened with losses compared to when they were incentivised with gains.

This divergence between positive or negative motivation and performance may relate to increased dopamine levels in the prefrontal cortex (PFC), which has been associated with heightened attention and cognitive stability (Arnsten, Wang, & Paspalas, 2012; Braver & Cohen, 2000; Cools, 2016; Cools & D'Esposito, 2011; Durstewitz & Seamans, 2008; Floresco, 2013; Ott, Jacob, & Nieder, 2014; Van Schouwenburg, Aarts, & Cools, 2010). Too much dopamine can 'overdose' the PFC, leading to decreases in attention and cognitive stability (Arnsten, 1998; Kimberg, D'Esposito, & Farah, 1997; Mattay et al., 2003; Phillips, Ahn, & Floresco, 2004), an effect which may explain the relative deterioration in performance when participants are incentivised with losses compared to gains (Cools, 2016).

Alternately, the divergent effect between the increased motivation and lack of effortful improvement associated with monetary losses may due to approach and avoidance associations; losses induce avoidance behaviour, and gains induce approach behaviour (Buzzell, Beatty, Paquette, Roberts, & McDonald, 2017; Houtman & Notebaert, 2013; Pratto & John, 1991). This effect can be seen in Go/NoGo tasks, where losses increase NoGo success rates but slow RTs relative to gains (Guitart-Masip et al., 2012). Differential effects of losses and gains on RTs may, therefore, be implicated in the inhibitory and preparatory components proposed by the horse-race model of motor actions (Band, Ridderinkhof, & van der Molen, 2003; Logan & Cowan, 1984; Schultz, 2015). The avoidance associations with losses should increase the strength of the inhibitory components, and the approach associations with gains should increase the strength of the preparatory components proposed by the model.

Our previous research (Byrne et al., 2020) showed that rewards can differentially improve motor activation and inhibition, indexed through power changes in alpha- and beta-band oscillations depending on task features. A decrease in power has been hypothesised to represent motor preparation in the sensorimotor cortex (Fox et al., 2016; Ishii et al., 2019; Pfurtscheller & Berghold, 1989; Tzagarakis, Ince, Leuthold, & Pellizzer, 2010; Tzagarakis, West, & Pellizzer, 2015). In contrast, an increase in power has been proposed to represent motor inhibition in the sensorimotor and frontal cortices (Fry et al., 2016; Jensen et al., 2005; Korzhik, Morenko, & Kotsan, 2018; Pfurtscheller, Stancak, & Neuper, 1996; Salmelin & Hari, 1994; Visani et al., 2019), especially an increase in the beta-band over frontal electrodes (Swann et al., 2009; Wagner, Wessel, Ghahremani, & Aron, 2018; Zavala et al., 2018).

The present study investigated the effects of rewards and losses on RTs and ERD patterns during a sustained vigilance task (Massar et al., 2016) and whether performance and cortical activation would be associated with the individual value of effort. Subjective value (SV) of effort was evaluated using a COGED task (Westbrook, Kester, & Braver, 2013). In the COGED task, participants were asked to decide in several iterations how much time would they be willing to spend on a task to gain or avoid losing a certain amount of money.

It was hypothesised that increasing gains and losses would cause faster RTs and increasing motor preparation reflected in stronger ERD patterns over frontal and sensorimotor regions and that cortical activation would be stronger and performance worse in trials offering avoiding a monetary loss compared to those offering a monetary gain. While our previous study (Byrne et al., 2020) did not find correlations between the SV of effort and performance or cortical activation, we predicted that such correlation could occur in trials entailing monetary losses.

5.3 Methods

5.3.1 Participants

25 subjects (13 females) were recruited. 4 subjects were removed from subsequent EEG analysis due to excessive muscle artefacts. Therefore, the final sample included 21 participants (11 females), aged 24.48 ± 3.97 (mean ± SD). The Research Ethics Committee of the University of Liverpool approved the procedure used, and all participants gave fully informed written consent at the start of the experiment, in accordance with the Declaration of Helsinki.

5.3.2 Procedure

Participants were required to complete two tasks; a modified version of the sustained vigilance task and a modified version of the discounting task used previously (Byrne et al., 2020; Massar et al., 2016). The trial structure of the tasks used can be seen in figure 5.1.

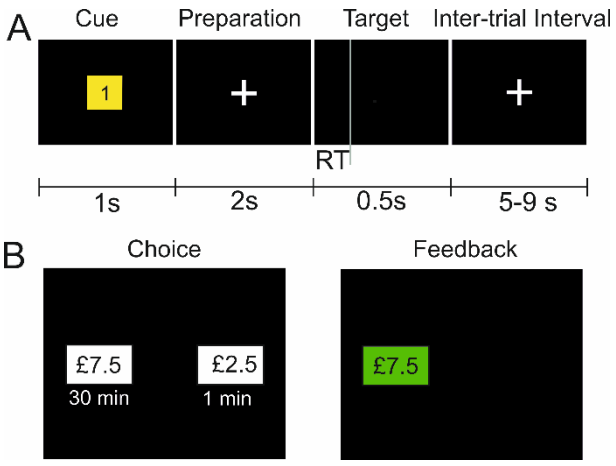

Figure 5.1. A schematic representation of trials presented to participants in the motivated vigilance task (A), and (B) the discounting choice task for both experiments.

The vigilance task consisted of four, fifteen-minute, blocks with of 100 trials each. There were five conditions in total, presented pseudo-randomly within blocks. Participants were offered a high or low reward for each fast response in the gain

conditions (5 p, or 10 p), a high or low punishment for each slow response in the loss conditions (-5 p, or -10 p), or were offered no reward (0 p). The effect of the incentive types on effort were assessed behaviourally using participants' mean RTs and electrophysiologically using the participants' changes in ERD in the 1-s epoch preceding the presentation of the target stimulus.

The discounting task was a modified version of the task used previously (Byrne et al., 2020; Massar et al., 2016; Westbrook et al., 2013), with loss conditions added, for the estimation of the subjective value (SV) of equivalent losses and gains in relation to different levels of effort.

5.3.3 Sustained vigilance task

The EEG net was first applied, then participants were taken into a dimly lit, sound-attenuated room and asked to complete the sustained vigilance task.

Similar to our previous study (Byrne et al., 2020), this task was an adaptation of the Psychomotor Vigilance Test (Dinges & Powell, 1985). Participants were first presented with a white fixation cross (baseline period) followed by a cue stimulus which displayed the reward offered for the next target stimulus (0 p, +5 p, +10 p, -5 p and -10 p), after which the fixation cross returned for two seconds before the target stimulus occurred (the fixation cross would disappear for 0.5 seconds). The inter-trial interval between the cue baseline period and the target stimulus was uniformly distributed and ranged from 3.5 to 9 seconds (see Figure 5.1A).

The participants first completed a practice block of the test, which lasted for 15 trials with no rewards offered. Their median RT was calculated during the practice block, then recalculated separately for each reward condition following each trial in the experimental portion of the task.

Following the same method as our previous study, trials were divided in half, whereby trials which participants responded faster than their median RTs were encoded as ‘fast’ trials and trials where participants responded slower than their median RTs were encoded as ‘slow’ trials.

During the experimental period of the task, participants were presented with 80 stimuli for each condition, meaning that the participants were offered a total gain or loss of £0, £4, or £8 if they earned the reward on every trial. The order of trials was pseudo-randomly rearranged at the start of each set of 5 trials, resulting in an equal number of trials for each condition and participants could not predict the next trial.

5.3.4 Discounting task.

Following the vigilance task, the discounting task was used to evaluate the subjective cost of cognitive effort (Massar et al., 2016; Westbrook et al., 2013). The task yields the value of the indifference point, defined as the average of the largest amount for which the participants chose the low-effort option and the lowest amount for which the participants chose the high-effort option.

Participants were presented with several pairs of monetary gains (up to £12) or monetary losses (up to £12), each pair consisted of one lower monetary offer and one higher monetary offer (Figure 5.1B). The participants were also given the choice between a low-effort option (completing the task again for 1 minute) or a high-effort option (completing the task again for 5, 10, 15, 20, 25, or 30 minutes). In the gain conditions, the low effort option was always accompanied by a smaller monetary gain when compared to the high effort option, whereas in the loss conditions, the high effort option was always accompanied by a smaller monetary loss when compared to the low effort option. After each choice, the monetary reward for each pair of offers was adjusted following a staircase titration method (i.e., in the gain condition the low-effort

option was increased if the high effort option was chosen and decreased if the low effort option was chosen). The amount of money added to, or taken away from, the offers was halved each time the participant made a choice. In gain conditions, participants were first offered £5 for the low-effort choice and £12 for the high effort option with an extra £2.50 being added to, or taken away from, the low effort options, depending on their choices. Similarly, in the loss conditions, participants were first offered a loss of £5 for the high-effort option, and a loss of £12 for the low-effort option, with an extra £2.50 being added to, or taken away from the high-effort options, depending on their choice. Participants made six choices during each effort condition (5, 10, 15, 20, 25, 30 minutes) for both gains and losses separately, and the order of conditions was randomly presented for each participant.

Once the participants had responded to all the choices, one choice was randomly selected. The participants were then required to complete the vigilance task at the level of effort chosen by the participant during the selected choice and received the associated amount of money.

In order to control for temporal discounting, participants were informed that they would be required to remain in the laboratory for the full 30 minutes in total, including the time spent completing the task; ensuring that the participants made decisions during the discounting task based upon the effort required, rather than the time taken to complete the task. While the effect of boredom associated with remaining in the lab was not directly investigated, all participants discounted higher levels of effort (30 mins) more than lower levels of effort (5 mins), meaning that they were reluctant to complete the task for longer period of time.

An indifference point was calculated for each effort and reward condition, defined as the average of the largest low-effort monetary offer for which the participant

chose the low-effort option, and the lowest low-effort monetary offer for which the participants chose the high-effort option (Massar et al., 2016; Westbrook et al., 2013).

The area under the curve (AuC) in the function representing associations between units of efforts and requested payoffs was computed in every participant (Myerson, Green, & Warusawitharana, 2001) for gain and loss trials separately. This measure corresponds to SV of effort and has been found to be correlated with need for cognition scores (Westbrook et al., 2013). The difference between this measure when participants were incentivised with losses or gains was compared using a paired sample t-test. A bivariate correlation was conducted to assess the relationship between this function, and RTs and ERD values.

5.3.5 EEG Recordings.

EEG data were recorded continuously using a 129-channel Geodesics EGI system (Electrical Geodesics, Inc., Eugene, Oregon, USA) with a sponge-based HydroCel Sensor Net. The net was aligned with reference to three anatomical head landmarks: two preauricular points and the nasion landmark. Electrode-to-skin impedances were kept below 50 kΩ and were kept at equal levels across all electrodes, a recording band-pass filter was set at 0.001 – 200 Hz with a sampling rate of 1000 Hz, and the Cz electrode was used as a reference electrode.

5.3.6 EEG data pre-processing.

A recording band-pass filter was set at 0.001-1000 Hz, with a sampling rate of 1000 Hz. Eye blinks and electrocardiographic artefacts were removed using principal component analysis (Berg & Scherg, 1994), and trials containing muscle artefacts in a visual inspection were excluded from subsequent analysis.

The average number of trials accepted for EEG analysis in each condition was: -10 p, 61.2 ± 18.57 (mean ± SD); -5 p, 60.16 ± 18.37 (mean ± SD); 0 p, 60.2 ± 17.87 (mean ± SD); +5 p, 62.16 ± 18.79 (mean ± SD); +10 p, 59.16 ± 18.40 (mean ± SD). The average number of accepted trials did not differ across conditions ($p > .05$). EEG data was pre-processed using BESA v 7.0 (MEGIS GmbH, Germany), and was re-referenced using a common average reference method (Lehmann, 1984), restoring the signal at electrode Cz.

5.3.7 Event-related desynchronization analysis

EEG signals were down-sampled to 256 Hz and power spectra was computed in Matlab (The Mathworks, Inc., USA) using Welch's power spectral estimate method. The power spectral densities were computed in 1-s segments (256 points) which were smoothed using a Hanning window prior to computing power spectrum. Power spectral densities were computed over 80 time points covering every 9-s trial. An array of 80 power spectra was obtained by shifting the 1-s spectral window over 9-s of EEG data with 0.1 s steps. The power spectral densities had frequency resolution of 1 Hz. The absolute power in selected frequency bands was transformed to ERD values (Pfurtscheller & Aranibar, 1977) using the epoch -1.5 s to -0.5 s to estimate the resting levels of cortical oscillations and the epoch ranging from 2-3 s after cue onset for activation.

5.3.8 Statistical analysis.

The differences in the median RTs across the five reward conditions and the two speed conditions of the vigilance task were compared using 2×5 repeated measures ANOVAs with five levels of reward (-10 p, -5 p, 0 p, +5 p, +10 p), and two levels of response-speed (fast and slow). For the choice task, the area under the curve

in the function representing associations between units of efforts and requested payoffs was computed in every participant (Myerson et al., 2001). This measure corresponds to SV of effort and has been found to be correlated with need for cognition scores (Westbrook et al., 2013).

To tackle the risk of a false positive error being made due to a large number of repeated tests, a hypothesis-independent permutation analysis was implemented in the *statcond.m* program in the EEGLAB package (Makeig, Debener, Onton, & Delorme, 2004). This was used to identify electrode clusters with significant main-effect or interactions of reward and response-speed (Maris & Oostenveld, 2007).

This cluster-based method provides a data-driven approach to assess effects of conditions on ERD in specified frequency bands (8-12 Hz, 16-24 Hz, and 4-7 Hz) across all electrodes without making a priori assumptions, while also controlling for multiple comparisons with no loss in statistical power.

The steps made in the permutation analysis are as follows. We first calculated the t-statistics for the main effects and interactions of reward and response-speed on ERD in the specified frequency band over all electrodes. ERD values in all experimental conditions were then collated into a single dataset, from which datapoints were randomly drawn and placed into subsets with the same size as the two response-speed and five reward conditions. This created a 'random partition' representing randomly shuffled versions of the reward and response-speed conditions. Next, the t-statistics for the main effects and interactions of reward and response-speed were calculated using the shuffled data in the random partition. The steps involving the creation and analysis of the random partition were then repeated 5000 times, and the proportion of random partitions that resulted in a larger t-statistic than the one first calculated for the original non-shuffled data was defined as the p-value. Finally,

electrodes which exceeded a predefined threshold regarding the p-values calculated (uncorrected $p < .01$) for the main effects or interactions of reward and response-speed were selected and clustered based on spatial adjacency.

T-tests with significance thresholds of 0.01 were also used to test whether ERD changes over each electrode were significantly different from 0, and electrode clusters showing statistically significant effects in both the permutation analyses and the t-test were explored further in SPSS v. 22 (IBM Inc., USA).

ERD changes were investigated separately in the alpha (8-12 Hz), beta (16-24 Hz), and theta (4-7 Hz) frequency band in the selected electrode clusters using 2×5 repeated measures ANOVAs, with Greenhouse-Geisser epsilon corrections being used to tackle any violations of sphericity in the data.

Further, to investigate the difference in the slope of the trend across gain (0 p, +5 p, +10 p) and loss (-10 p, -5 p, 0 p) conditions, linear regressions were calculated for RTs and ERD values in each electrode cluster for gains and losses separately. The slope of the linear trend was compared across gain/loss and response-speed conditions using 2×2 repeated measures ANOVAs, and the relationships between RTs and ERD regression slopes in gain and loss conditions were compared using bivariate correlations.

The ERD and RT difference variables were correlated with each other and individual AuC of SVs using bivariate correlations. Bivariate correlations were conducted in all electrode clusters or single electrodes selected for further analysis, however, only statistically significant correlation coefficients are reported.

5.4 Results

5.4.1 Vigilance task

Mean RTs for fast and slow trials and across the five reward conditions are shown in Figure 5.2. Differences in reaction times across the five reward conditions (-10 p, -5 p, 0 p, +5 p, +10 p), and across both fast and slow trials were analysed using a 2×5 repeated measures ANOVA. A statistically significant main effect of reward was found ($F(4, 21) = 3.77$, $p = .02$, $\eta p^2 = .25$), with RTs in the 0 p reward condition being significantly slower than the RTs in any of the gain or loss conditions. RTs in the high-reward/loss conditions (-10 p, +10 p) were also significantly faster than RTs in the low-reward/loss conditions (-5 p, +5 p) ($p < .05$).

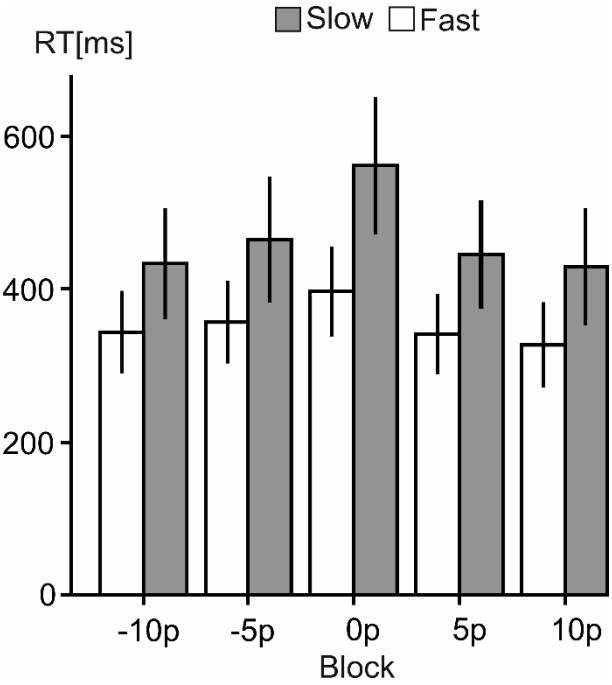

Figure 5.2. A bar chart to show the mean RTs in each reward condition (0 p , 5 p, 10 p) in slow (grey) and fast (white) trials. Error bars represent the standard errors of the mean.

The profile of mean RTs in the five reward conditions formed an inverted U shape, and a statistically significant quadratic trend was found ($F(1,20) = 13.77$, $p = .001$, $\eta p^2 = .37$). There was no significant difference ($p > .05$) between the individual

slopes of the descending linear trend in the loss domain (-10 p, -5 p, 0 p) and the individual slopes of the ascending linear trend in the gain domain (0 p, 5 p, 10 p). However, a significant positive correlation was found between the two slopes ($r(19) = .93$, $p < .001$). This suggests that both incentive types caused similar shortening of responses under increasing incentive magnitude, and that participants who showed similar shortening of RTs under increases in gains also showed a similar shortening of RTs under increasing losses.

Changes in RTs across reward and response-speed conditions were correlated with the values of effort in gain and loss domains, evaluated as the AuC, calculated separately for gain and loss conditions in individual COGED curves representing the indifference points calculated in each of the six task durations. No statistically significant correlations, however, were found between changes in RTs and the AuC calculated in either the gain or loss domain.

5.4.2 Discounting task

A linear regression analysis was used to compare the change in SV for each effort condition (5, 10, 15, 20, 25 & 30 minutes) in both gain and loss conditions. The mean discounting values across offered 5-30 min task durations for gain and loss conditions are shown in Figure 5.3A.

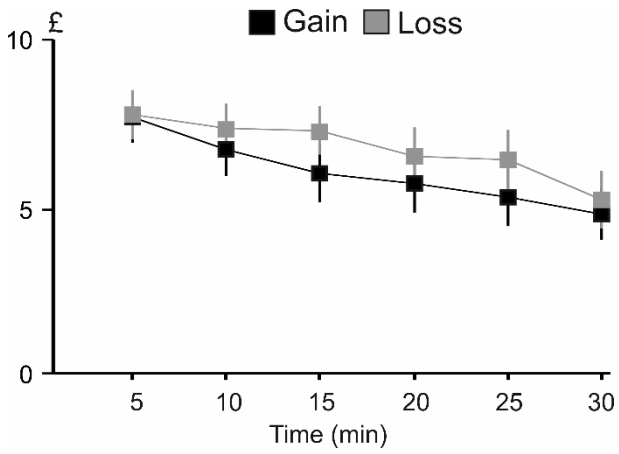

Figure 5.3. A line graph to show the discounting curve in the choice task, with the mean subjective value shown for each block in the task (5, 10, 15, 20, 25, 30 minutes) (A), and a bar chart to represent the mean area under the curve (%) values found in the discounting task for gain and loss conditions (B). Error bars represent standard errors of the mean.

In gain conditions, there was a significant negative linear relationship between the levels of effort and SVs ($F(1, 148) = 31.57$, $p < .001$, $\boldsymbol{R^2} = .42$). The regression model showed a negative linear regression with an equation of:

$$Y = -.109X + 7.93 + \varepsilon,$$

Where Y is the SV, X is the effort level, and ε is an error element.

Similarly, in loss conditions, there was a significant negative linear relationship between the levels of effort and SVs ($F(1, 148) = 23.62$, $p < .001$, $\boldsymbol{R^2} = .132$). The regression model showed a negative linear regression with an equation of:

$$Y = -.094X + 8.384 + \varepsilon,$$

A one samples t-test was conducted to compare the mean AUC of the SVs of effort associated with gain and loss conditions. The t-test found a statistically significant difference between gain and loss conditions in AuC ($F(1, 24) = 17.98$, $p < .001$), showing that losses were subjectively more motivating than gains. AUC differences between gain and loss conditions are shown in Figure 5.3.

5.4.3 ERD patterns across trials

Figure 5.4 (A-C) shows the time courses and topographic of alpha, beta and theta ERD/ERS across trials, respectively. Oscillations during the cue interval (0.5 s after cue onset) were featured by an ERD over occipital electrodes in the alpha band (Figure 5.4A), an effect consistent with the presence of attentional and visual processing of a reward cue.

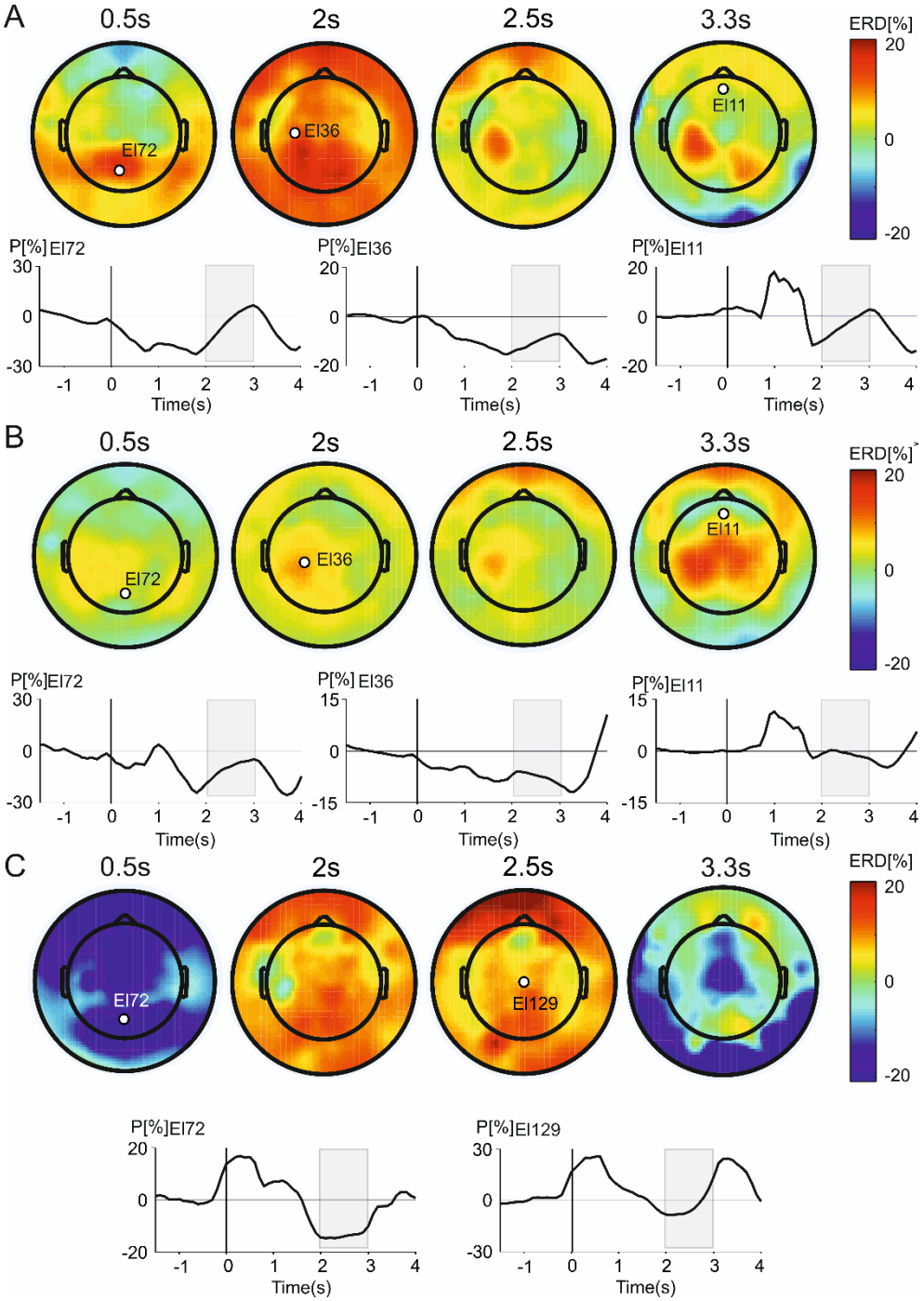

Figure 5.4. Topographic maps of alpha (A), beta (B) and theta (C) ERD at four time points: during presentation of visual cue (0.5 s), an early period of anticipation of motor response (2 s), late period of motor response anticipation (2.5 s), and during the motor response (3.3 s). In each section (A-C), ERDs at selected electrodes are also shown. The grey rectangles covering the interval from 2 s to 3 s represent the epoch of interest preceding the motor response.

During the period of motor readiness (2 s and 2.5 s after cue onset in Figure 5.4 (A-C), alpha and beta ERD were prominent in left (contralateral) parietal

electrodes. During the time of motor response (3.3 s after cue onset) alpha- and beta-ERD was distributed bilaterally over central and parietal electrodes. In the theta-band (Figure 54C), activation during the presentation of the cue stimulus (0.5 s after cue onset) was dominated by the presence of a phase-locked evoked response causing an increase in power over the whole scalp. The period of motor activation (3.3 s after cue onset) was characterised by a prominent theta-ERS at central and precentral midline electrodes; these components were related to the phase-locked potentials in response to visual cue and movement execution.

5.4.4 Alpha-band ERD

The grand average topographic maps showing alpha-band ERD for all trials as well as the electrodes found to be significantly different from 0 are shown in Figure 5.5A. One cluster of electrodes in the left central area, and one frontal electrode showed alpha ERD surpassing the combined amplitude and statistical thresholds. Topographic maps showing ERD in each of the three reward conditions are shown in Figure 5.5B for slow trials, in Figure 5.5C for fast trials, and Figure 5.5D for all trials irrespective of the speed of motor responses.

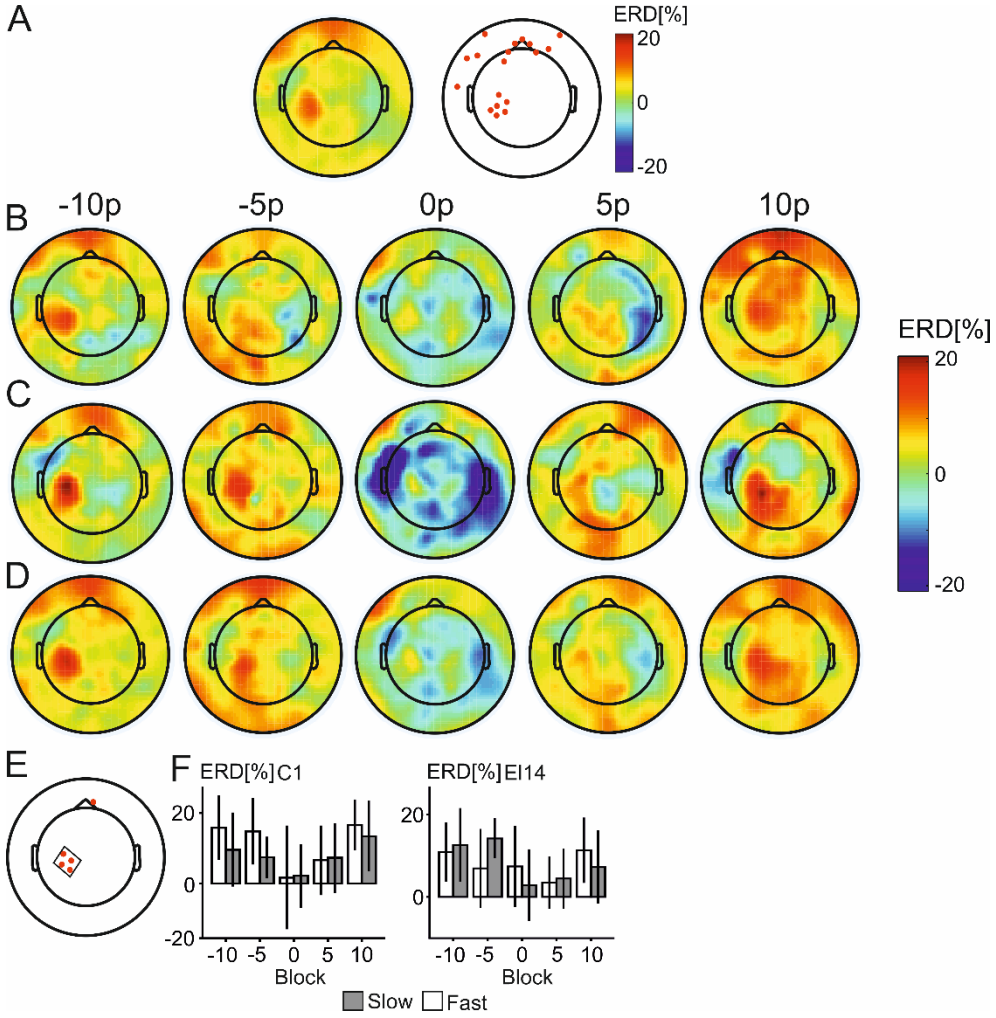

Figure 5.5. Alpha-band ERD during the anticipation of motor response. Topographic map of alpha-band ERD across all conditions and trials (left), and electrodes showing a robust alpha-band ERD across all conditions (right) (A). Topographic maps of alpha-band ERD in each of the five reward conditions during slow RT trials (B). Topographic maps in each of the five reward conditions in fast RT trials (C). Topographic maps in each of the five reward conditions across all trials (D). Location of electrodes in the two clusters manifesting statistically significant main effects of reward (E), and bar charts showing mean alpha-band ERD in each of the five reward conditions in slow (grey) and fast (white) RT trials. Error bars represent standard error of the mean (F).

To investigate the effects of response-speed and reward on ERD values, 2×5 repeated measures ANOVAs were computed to assess the significant main effects and interactions of response-speed (fast & slow) and reward (-10 p, -5 p, 0 p, +5 p, +10 p) on ERD values.

A statistically significant main effect of reward was found in a cluster of four electrodes overlying the contralateral sensorimotor cortex and in one electrode located in the frontal region of the scalp (Figure 5.5E). The main effect of reward in the left-central cluster of electrodes (cluster 1) ($F(4, 24) = 3.49$, $p = .029$, $\eta p^2 = .15$) was due to a significantly stronger ERD in all gain and loss conditions compared to the no-reward condition ($p < .05$).

The pattern of mean ERD values in this cluster followed a U-shaped profile, with a statistically significant quadratic trend ($F(1,20) = 5.47$, $p = .03$, $\eta p^2 = .22$). A significant positive correlation was found between individual ascending slopes for losses conditions and individual ascending slopes for gain conditions ($R(19) = .73$, $p < .001$), but no significant difference was found between the two sets of slopes ($p > .05$).

The significant main effect of reward found in the frontal electrode (electrode 14) ($F(4, 24) = 3.28$, $p = .022$, $\eta p^2 = .14$) was the result of ERD found in the 0 p trial being significantly smaller than that found in the loss conditions (-5 p, -10 p) and the large gain condition (+10 p). No significant difference ($p > .05$), however, was found between the ERD found in the no-reward condition and the small gain (+5 p) condition ($p > .05$).

Similar to cluster 1, the U-shaped trend manifested as a statistically significant quadratic trend ($F(1, 20) = 6.56$, $p = .02$, $\eta p^2 = .25$), with a significant positive correlation ($r(19) = .72$, $p < .001$) but no significant difference ($p > .05$) between the gradient of the gain and loss slopes.

To test the association between ERD results in the alpha band and behavioural results, difference variables were calculated, representing the mean difference between ERD found in gain conditions (+10 p, +5 p,) and the no incentive condition (0 p), and

the difference between the ERD found in loss conditions (-5 p, -10 p) and the no incentive condition (0 p). However, no statistically significant correlations were found between these difference variables and the difference variables created for RTs, or the AuC of individual discounting curves.

5.4.5 Beta-band ERD

The grand average topographic map for all trials and the distribution of electrodes showing an ERD significantly different from zero are shown in Figure 5.6A. ERD in the beta band was characterised by a focus over contralateral central and parietal electrodes (Figure 5.6D). The spatial ERD focus was stronger and more widespread in higher loss/gain conditions and in fast (Figure 5.6C) compared to slow (Figure 5.6B) trials. Notably, ERD patterns were similar in both loss conditions (-10 p and -5 p) but stronger in the +10 p than +5 p gain condition.

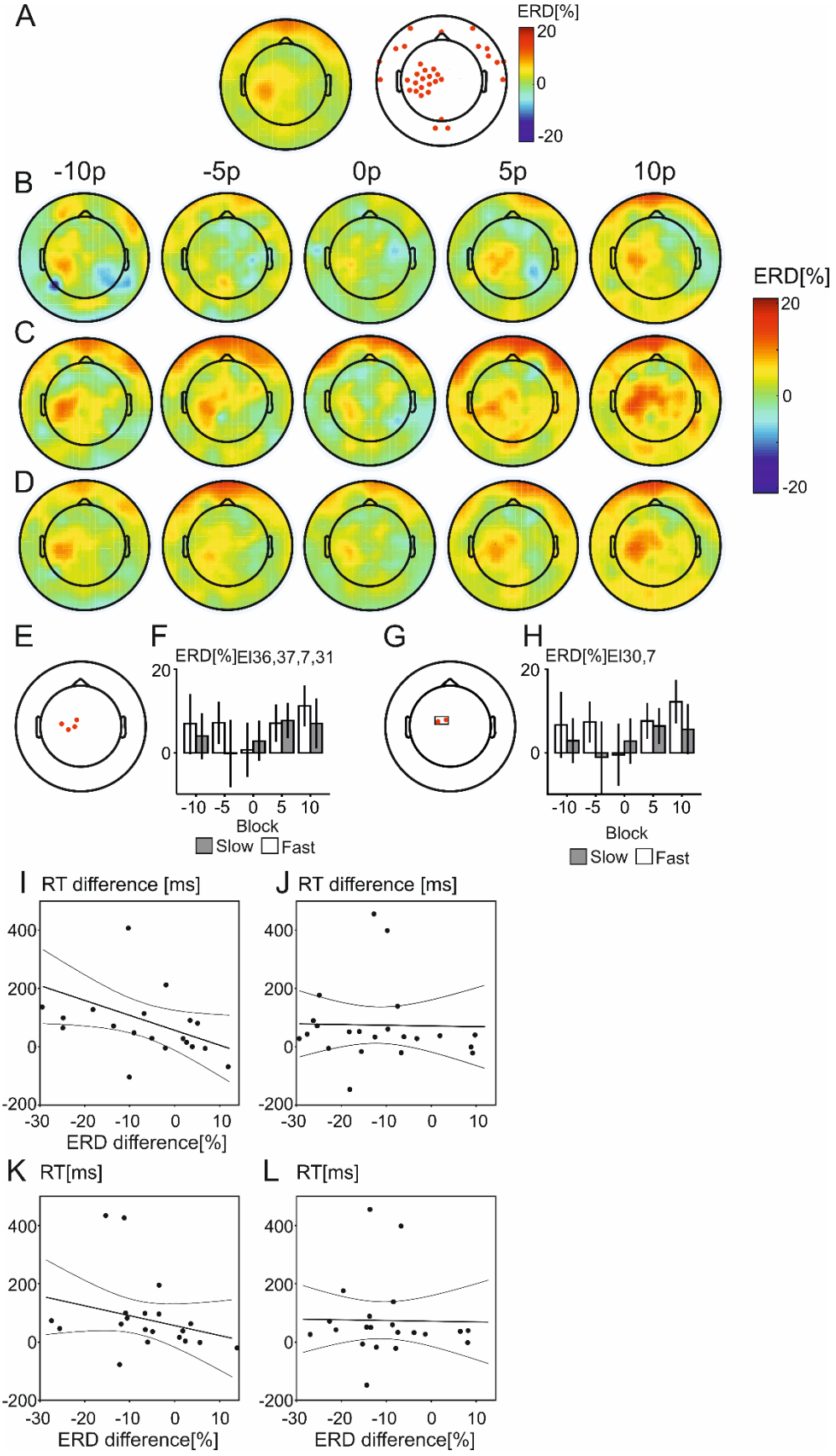

Figure 5.6. Beta-band ERD during the anticipation of motor response. Topographic map of beta-band ERD across all conditions and trials (left), and

electrodes showing a robust beta-band ERD across all conditions (right) (A). Topographic maps of beta-band ERD in each of the five reward conditions during slow RT trials (B). Topographic maps in each of the five reward conditions in fast RT trials (C). Topographic maps in each of the five reward conditions across all trials (D). Location of electrodes in the cluster manifesting statistically significant main effects of reward (E), and bar charts showing mean beta-band ERD in each of the five conditions in slow (grey) and fast (white) RT trials. Error bars represent standard error of the mean (F). Scatterplots and the linear regression line with 95% confidence intervals illustrating the statistically significant correlation between beta-band ERD differences and RT differences (all incentive conditions – no reward condition) in gain trials in electrodes 36, 37, 7, and 31 (I), and the non-significant correlation in loss trials (J), as well as correlations in electrodes 30 and 7 in gain (K) and loss (L) trials.

Two clusters of electrodes showing a statistically significant main effect of reward (Figure 5.6E) or response-speed (Figure 5.6G) were found in the left (contralateral) central electrodes overlaying the sensorimotor cortex. The first cluster of electrodes showed a significant main effect of reward, while the second cluster, which shared one electrode and a similar main effect of reward with the first cluster, also showed a significant main effect of response speed. The two electrodes in the second cluster were on the anterior side of the first, suggesting that they were recording activation from the motor cortex directly relating to movement. Consistent with previous research (Salmelin & Hari, 1994; Stancak & Pfurtscheller, 1996), both clusters were marginally more anterior (Figures 5.6E and G) than the cluster of electrodes selected in the alpha band (Figure 5.5E).

The significant main effect of reward found in cluster 1 (Figure 5.6E) ($F(4, 24) = 3.20$, $p = .024$, $\eta p^2 = .14$) was due to ERD in the 0 p reward condition being significantly smaller than the ERD found in both the +5 p ($p = .016$) and the +10 p ($p = .007$) conditions, and stronger in the +10 p condition compared to the -5 p condition ($p = .04$).

In this cluster, a significant quadratic trend was found ($F(1,20) = 5.24$, $p = .03$, $\eta p^2 = .21$), as well as a significant positive correlation between the individual

ascending slopes across loss conditions and descending slopes across gain conditions (r(19) = .62, p = .003). However no significant difference was found between the ascending linear trend in loss conditions and the descending linear trend in gain conditions.

Cluster 2 (Figure 5.6G) shared one electrode with cluster 1, and showed a similar main effect of reward (F(4, 24) = 2.90, p = .038, $\boldsymbol{\eta p^2}$ = .13), with significantly smaller ERD in the 0 p reward condition than that in both the +5 p (p = .022) and +10 p (p = .009) conditions. No significant difference, however, was found between ERD found in 0 p conditions and that in either the -5 p or -10 p condition (p > .05). In addition to these effects of reward, the two electrodes in this cluster also showed a significant main effect of response speed not seen in cluster 1, where ERD preceding fast responses was significantly stronger than that preceding slow responses (F(1,20) = 6.72, p = .017, $\boldsymbol{\eta p^2}$ = .25)

Similar to cluster 1, cluster 2 showed a significant main effect of reward (F(4, 24) = 2.90, p = .038, $\boldsymbol{\eta p^2}$ = .13) due to ERD in the 0 p reward condition being significantly smaller than in the +5 p (p = .022) and the +10 p conditions (p = .009). There was no significant difference between ERD found in the 0 p reward condition, and ERD found in either the -5 p or -10 p conditions (p > .05) suggesting an asymmetric effect of reward magnitude on ERD patterns in loss and gain domains. Cluster 2 showed an effect of respond speed not seen in cluster 1 due to ERD in fast trials was significantly larger than the ERD found in slow trials (F(1,20) = 6.72, p =.017, $\boldsymbol{\eta p^2}$ = .25).

A U-shaped curve was found with a statistical significant quadratic trend (F(20, 1) = 5.95, p = .02, $\boldsymbol{\eta p^2}$ = .23), with a significant positive correlation (r(19) = .61, p = .003) but no significant difference between the gradient of the gain and loss slopes.

In order to evaluate the relationship between behavioural results and beta-ERD found in cluster 1, a difference variable was created representing the mean difference between the ERD found in the 0 p condition and the +5 p and +10 p conditions collectively (0 p - +5/10 p). A similar difference variable was also calculated for individual RTs. A statistically significant negative correlation was found between the difference variables calculated for RTs and for beta-band ERD in gain conditions ($r(19) = -.43$, $p = .049$), however no significant correlations were found in loss conditions ($p > .05$). Figure 5.6I shows the correlations between RT and ERD changes in gain conditions, and Figure 5.6J shows the correlations between RT and ERD changes in loss conditions.

Difference variables were also calculated in this cluster, as the mean difference between RTs and ERD in gain/loss conditions (5 p, 10 p) and in the 0 p condition, however, no significant correlations were found in cluster 2. The results of this correlation in gain conditions are shown in Figure 5.6K and in loss conditions in Figure 5.6L.

The relationship between ERD in the beta-band and discounting results was assessed by calculating difference variables representing the mean difference between ERD found in gain conditions (+5 p, +10 p) and the no incentive condition and between ERD found in loss conditions (-5 p, -10 p) and the no incentive condition. No correlation, however, was found between the AuC of individual discounting curves and ERD difference variables in the beta-band.

5.5 Discussion

The present study investigated the effect of graded positive and negative incentives on effortful performance and anticipatory cortical oscillatory activity during a cued vigilance RT task. We found that RTs and ERD in scalp regions overlaying the

sensorimotor and frontal cortex showed incentive-related changes forming a 'U-shaped' curve, with no significant difference between gradient of the slopes in loss and gain trials. While both RTs and beta-band ERD showed similar changes across increasing values of reward in gain and loss domains, RTs and beta-band ERD were correlated in a cluster of electrodes overlying the contralateral sensorimotor cortex only in gain but not in loss domain. However, while losses were more motivating than gains, individual SVs of effort in loss and gain domains did not correlate with changes in performance or ERD values.

Matching the trend found in RTs, ERD in the alpha and beta bands over sensorimotor areas of the scalp, and over frontal regions of the scalp in the alpha band, showed graded increases to both positive and negative incentives, forming a 'U-shaped' curve. ERD over sensorimotor areas in the alpha and beta bands is commonly observed seconds before movement initiation and likely represents motor preparation (Chatrian, Petersen, & Lazarte, 1959; Fox et al., 2016; Ishii et al., 2019; Pfurtscheller & Berghold, 1989; Stancak & Pfurtscheller, 1996; Tzagarakis et al., 2010; Tzagarakis et al., 2015). Alpha-band ERD over frontal regions may relate to activation in the frontoparietal control network, where frontal regions are posited to provide top-down control of anticipatory attention in visual and posterior parietal regions of the brain (Corbetta, Patel, & Shulman, 2008; Coull, Walsh, Frith, & Nobre, 2003; Kastner & Ungerleider, 2000; Serences & Yantis, 2006). This network has been linked to alpha-band ERD over frontal regions, with the disruption of alpha-band oscillations over frontal areas of the scalp being shown to impair participants' ability to identify a visual stimulus displayed two seconds later (Capotosto, Babiloni, Romani, & Corbetta, 2009).

The present study suggests that both motor preparation and anticipatory attention increased with larger incentives, regardless of whether the incentives were losses or gains. This falls in line with the classical finding of a 'U-shaped' relationship between the effects of losses and gains on arousal, with both increasing arousal levels (Bechara, Damasio, Tranel, & Damasio, 1997; Costantini & Hoving, 1973; Davidson, Ekman, Saron, Senulis, & Friesen, 1990; Ganzach & Karsahi, 1995; Hochman & Yechiam, 2011; Lang, Bradley, & Cuthbert, 1990, 1997; Sokol-Hessner, Camerer, & Phelps, 2013). The present results expanded this classical observation to RT performance and provided the novel measure of anticipatory ERD, showing that incentives increased task engagement through the heightened anticipatory attention required to detect the target stimulus quickly and the increased motor preparation required to respond as fast as possible once the target stimulus was detected.

While losses were found to be more motivating than gains, no difference was found between the gradient of RTs and anticipatory ERD slopes with increasing losses and gains. This suggests that gains and losses of equal nominal value caused similar improvements in effortful behaviour, but also that graded increases in the two incentive types were associated with similar slopes of increasing effortful performance and anticipatory cortical responses.

An asymmetry in the effects of gains and losses manifested in the presence of a statistically significant positive correlation between beta-ERD in electrodes overlying the contralateral sensorimotor cortex and RTs in the gain, but not loss domain. This positive correlation, in spite of symmetric increases in cortical activation across loss and gain levels, suggests that performance is adjusted proportionally to the preparatory activation of the sensorimotor cortex in anticipation of a gain, but more loosely in the anticipation of a loss. Losses have been shown to be more motivating

than gains (Baumeister, Bratslavsky, Finkenauer, & Vohs, 2001; Krebs & Woldorff, 2017; Rozin & Royzman, 2001; Wright & Rakow, 2017), but often do not improve performance relative to gains (Carsten et al., 2018; Paschke et al., 2015; Potts, 2011). It has been hypothesised that losses cause stronger arousal (Hochman & Yechiam, 2011; Lang et al., 1997; Low, Lang, Smith, & Bradley, 2008), as evidenced by increased pupil dilation (Hochman & Yechiam, 2011), autonomic arousal (Vaish, Grossmann, & Woodward, 2008), and anterior cingulate activation (Frank, Woroch, & Curran, 2005; Yeung, Botvinick, & Cohen, 2004). Losses may, therefore distract participants from the primary task goals or cause 'choking under pressure' (Ariely, Gneezy, Loewenstein, & Mazar, 2009; Beilock, 2010; Bonner, Hastie, Sprinkle, & Young, 2000; Camerer, Hogarth, Budescu, & Eckel, 1999; Mobbs et al., 2009; Samuels & Whitecotton, 2011; Worthy, Markman, & Maddox, 2009; Zedelius, Veling, & Aarts, 2011). The present results suggest that losses may lead to a disbalance between cortical activation and subsequent RTs due to them producing greater arousal than equivalent anticipated gains.

Consistent with the findings of our previous experiment (Byrne et al., 2020), beta-band ERD over sensorimotor regions was significantly stronger when preceding a fast compared to a slow moment. This supports the hypothesis that beta-band ERD relates directly to movement preparation (Fry et al., 2016; Ishii et al., 2019; Little, Bonaiuto, Barnes, & Bestmann, 2018; Neuper & Pfurtscheller, 2001; Palmer, Zapparoli, & Kilner, 2016; Tewarie et al., 2018), whereas alpha-band ERD reflects the executive planning and control of movements (Calton, Dickinson, & Snyder, 2002; Fumuro et al., 2015; Naranjo et al., 2007; Prado et al., 2005), suggesting that fast movements required stronger direct motor preparation than slow movements. This contrasts with previous studies which show no effect of contraction force (Cremoux,

Tallet, Berton, Dal Maso, & Amarantini, 2013; Stancak, Riml, & Pfurtscheller, 1997), movement speed (Fry et al., 2016; Stancak & Pfurtscheller, 1995), and movement length or direction (Tatti et al., 2019) on pre-movement ERD in the beta band. However, a stronger ERS following fast compared to slow movements has been found (Fry et al., 2016; Parkes, Bastiaansen, & Norris, 2006; Stancak et al., 1997), indicating that greater inhibition is required to supress motor activation following the cessation of faster movements. The deviation from previous results may be explained by difference in task demands, where response speed was not dependent on instructions given to participants, but rather by incentives offered or trial-by-trial variations in attention or motor preparation. Stronger sensorimotor ERD in the beta band in fast trials may therefore be reflective of changes in motor preparation under conditions of high motivational relevance, perhaps being the result of fast responses perhaps recruiting larger muscle groups or ERD in slow trials reflecting a state of idling in sensorimotor regions.

Individual SVs of effort calculated during the discounting task in loss and gain conditions did not significantly correlate with either the speeding of RTs or the increase in anticipatory ERD with increasing losses or gains. Similar results were also found in our previous study (Byrne et al., 2020), with no significant correlation being found between the SVs of effort and the shortening of RTs or changes in cortical oscillations under increasing reward. It is, therefore, likely that an individual's willingness to engage in effortful tasks when incentivised with monetary gains or threatened with monetary losses does not directly inform effortful performance when they are offered either positive or negative incentives. Incentives may, instead, influence performance through other variables, such as the approach/avoidance associations made with the incentive (Buzzell et al., 2017; Houtman & Notebaert,

2013; Pratto & John, 1991), or their effect on cognitive frames (Brooks, Stremitzer, & Tontrup, 2017; Church, Libby, & Zhang, 2008; Gose & Sadrieh, 2012; Hannan, Hoffman, & Moser, 2005; Van de Weghe & Bruggeman, 2006). Alternatively, these findings fall in line with the attentional model of loss-aversion (Yechiam & Hochman, 2013), which posits that losses capture greater attention than gains, leading to more loss-averse behaviour in the choice task without losses incentivising increased effortful control during the sustained vigilance task compared to gains..

It should be noted, that while the linear trend of gains and losses was directly compared, only two levels of each incentive type (+/-5 p and +/-10 p) as well as the no incentive condition (0 p) were used. The exact shape and slope of the linear trend, therefore, could not be established to a high degree of resolution. Further, the largest incentive offered was a loss or gain of 10 p. This amount may not have been large enough to elicit a strong approach or avoidance response, which may explain the similarities between losses and gains found presently. It is suggested that future research investigates the 'U-shaped' effect of losses and gains on effortful performance and cortical oscillatory responses with additional incentive conditions such as 1 p or 50 p conditions in gain and loss trials to establish this trend with more detail.

5.6 Conclusions

The present study demonstrates symmetrical increases in effortful performance and cortical activation while preparing a speeded RT response during a sustained vigilance task, with no significant differences between losses and gains. Neural activation in sensorimotor areas, evaluated using amplitude changes in cortical oscillations, is related to response speeds and the magnitude of expected positive or negative incentives. The value of effort, however, does not map onto preparatory

changes of spontaneous cortical activation. This suggests that the value of effort may affect the decision to engage in a task but not the instantaneous control of speeded RT movements.

Chapter 6

Investigating the effect of losses and gains on effortful engagement during an incentivised Go/NoGo task through anticipatory cortical oscillatory changes.

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This experiment investigated the cortical oscillatory changes reflecting approach/avoidance motor responses when participants expected a loss or a gain, as well as an inhibitive or active motor response. This paper was submitted to the Journal of Psychophysiology.
The format of the text has been modified to match the style of this thesis.
The roles of the co-authors are summarised below:
I designed the study in collaboration with Andrej Stancak and collected the data. Danielle Hewitt, Jessica Henderson, Alice Newton-Fenner, Hannah Roberts, and John Tyson-Carr assisted with the collection of data and contributed useful comments whilst preparing the manuscript for publication. Andrej Stancak, Nick Fallon, and Timo Giesbrecht contributed to the experimental design as well as the large-scale planning of this project. Andrej Stancak and Timo Giesbrecht secured funding for project.

6.1 Abstract

Losses usually have greater subjective value (SV) than gains of equal nominal value but often cause a relative deterioration in effortful performance. Since losses and gains induce differing approach/avoidance behavioural tendencies, we explored whether incentive type interacted with approach/avoidance motor-sets. Alpha- and beta-band event-related desynchronization (ERD) was hypothesised to be weakest when participants expected a loss and prepared an inhibitory motor-set, and strongest when participants expected a gain and prepared an active motor-set. It was also hypothesised that effort would modulate reward and motor-set related cortical activation patterns.

Participants completed a cued Go/NoGo task while expecting a reward (+10p), avoiding a loss (-10p), or receiving no incentive (0p); and while expecting a NoGo cue with a probability of either .75 or .25. Premovement alpha- and beta-band EEG power was analysed using the ERD method, and the SV of effort was evaluated using a cognitive effort discounting task.

Gains incentivised faster RTs and stronger preparatory alpha band ERD compared to loss and no incentive conditions, while inhibitory motor-sets resulted in significantly weaker alpha-band ERD. However, there was no interaction between incentive and motor-sets. Participants were more willing to expend effort in losses compared to gain trials, although the SV of effort was not associated with ERD patterns or RTs.

Results suggest that incentive and approach/avoidance motor tendencies modulate cortical activations prior to a speeded RT movement independently, and are not associated with the economic value of effort. The present results favour attentional

explanations of the effect of incentive modality on effort.

6.2 Introduction

Effort can be conceptualised as a decision-making factor, where individuals decide to expend effortful resources on the promise of an anticipated reward, monetary or otherwise (Inzlicht, Schmeichel, & Macrae, 2014; Kurzban, Duckworth, Kable, & Myers, 2013). It would therefore be expected that effortful resources are deployed proportional to the value of an offered incentive, as supported by the observation that larger rewards encourage improved effortful performance compared to smaller ones (James, Reuther, Angus, Clarke, & Hunt, 2019; Massar, Lim, Sasmita, & Chee, 2016; Soutschek, Kang, Ruff, Hare, & Tobler, 2018).

Losses are generally found to be more motivating (Baumeister, Bratslavsky, Finkenauer, & Vohs, 2001; Krebs & Woldorff, 2017; Rozin & Royzman, 2001; Wright & Rakow, 2017), as well as being more arousing, than gains (Low, Lang, Smith, & Bradley, 2008; Sokol-Hessner et al., 2009; Stancak et al., 2015) and causing greater activation in cortical and striatal areas (Gehring & Willoughby, 2002; Holroyd & Coles, 2002; Tom, Fox, Trepel, & Poldrack, 2007; Yeung, Botvinick, & Cohen, 2004). It would thus be expected that losses cause an increase in performance relative to gains. However, monetary losses often cause no change (Boksem & Tops, 2008; Seifert, Naumann, Hewig, Hagemann, & Bartussek, 2006), or even a deterioration in effortful performance relative to gains of equal nominal value (Carsten, Hoofs, Boehler, & Krebs, 2018; Fontanesi, Palminteri, & Lebreton, 2019; Paschke et al., 2015; Potts, 2011).

We have investigated the effect of incentive on cognitive effort using a neuroeconomic approach and showed that effortful engagement under high incentives was associated with the increased desynchronization of cortical oscillations in the alpha band over posterior parietal and frontal regions of the scalp, and in the beta band over bilateral sensorimotor areas (Byrne et al., 2020). Event-related desynchronization (ERD) in the alpha band has previously been associated with anticipatory attention (Corbetta, Patel, & Shulman, 2008; Coull, Walsh, Frith, & Nobre, 2003; Kastner & Ungerleider, 2000; Serences & Yantis, 2006), while sensorimotor beta-band ERD has been associated with the maintenance of a prepared motor response (Fox et al., 2016; Ishii et al., 2019; Pfurtscheller & Berghold, 1989; Tzagarakis, Ince, Leuthold, & Pellizzer, 2010; Tzagarakis, West, & Pellizzer, 2015). In our subsequent study, we showed symmetrical increases in the speeding of RTs and preparatory cortical activation under graded gains and losses, despite losses being more motivating than gains (Byrne et al., submitted). However, we were unable to establish the underlying cause behind the divergent effect of losses and gains on effortful performance.

The divergent effect of losses and gains on effortful performance has been hypothesised to be the result of attentional biases associated with loses. According to the attentional model of loss aversion, losses may cause a relative deterioration in effortful performance because they distract participants from the primary task goals (Yechiam & Hochman, 2013). Alternately, the contradictory effect of gains and losses on performance has been suggested to be due to approach and avoidance associations made with losses and gains; gains induce approach behaviours and losses induce avoidance behaviours (Buzzell, Beatty, Paquette, Roberts, & McDonald, 2017; Hoofs, Carsten, Boehler, & Krebs, 2019; Houtman & Notebaert, 2013; Pratto & John, 1991).

The present study investigated the approach/avoidance and attentional tendencies associated with losses and gains during effortful engagement. We asked whether preparatory approach/avoidance motor sets would interact with, or act independent of, the cortical effect of positive and negative incentives on cortical oscillatory responses during effortful engagement. The main effects and interactions of positive/negative incentives and preparatory approach/avoidance motor sets on behavioural performance and anticipatory ERD performance were investigated during a cued Go/NoGo task, where incentive was modulated on a trial-by-trial basis (Krebs, Boehler, & Woldorff, 2010; Novak & Foti, 2015; Zhang, Li, Wang, Liu, & Zheng, 2017). It is important to note that RTs and NoGo stopping rates may not provide a direct measure of effortful engagement, and may be confounded by factors such as mood, ability, and strategy (Locke & Latham, 1990). ERD measures were therefore implemented to shed further light on the cortical processes underlying effortful performance under differing reward and task conditions.

The employment of decision-making approaches to evaluate the subjective value of effort is a comparatively novel development in the field of cognitive effort (Botvinick et al., 2009; Treadway et al., 2009; Kurniawan et al., 2010; Prévost et al., 2010), where it is proposed that the choice to engage in an effortful task results from the weighing of effort costs against the value of its outcomes (Westbrook and Braver, 2015; Kool et al., 2017; Shenhav et al., 2017). In discounting paradigms, participants are given the choice between a low-effort option for a small reward and a high-effort-option for a large reward. By measuring an individual's preference for high-effort options over a range of reward levels, their effort-discounting rates can be plotted on a discounting curve. Measuring the subjective value of effort directly reflects a number of methodological and theoretical challenges to decision-making paradigms (Massar

et al., 2016; Westbrook et al., 2013; Klein-Flügge et al., 2015; Warm et al., 1996). However, the effort value generated from discounting tasks has proved useful in predicting individuals' need for cognition scores (Westbrook et al., 2013).

Our study is a timely attempt to shed more light on how the subjective value of effort is mapped onto performance and cortical activation changes under differing incentives and task-conditions. The performance-based outcomes taken from the Go/NoGo task may not have been good measures of the subjective value of effort due to potential capacity limits, resulting in a ceiling effect (LeBouc et al., 2016). Similar to other studies (Massar et al., 2016; Westbrook et al., 2013), the subjective value of effort was evaluated using a decision-making experiment (COGED) offering trade-offs between the duration of the Go/NoGo task and the money that the participant would be willing to pay to avoid engaging in the task for a prolonged period of time. It was hypothesised that individual effort discounting rates, used as a proxy of their cognitive effort valuation, would manifest in shorter RTs when incentivised with a gain/loss, especially in Go-primed trials, and in stronger cortical activation changes sub-serving the execution of speeded RT movements.

Bolstering behavioural findings, ERD measures were chosen as the Go/NoGo task used presently required competing processes of motor activation and inhibition, and these measures are able to separate cortical activation (ERD) from inhibition (ERS). Specifically, ERD in the alpha and beta bands is found over somatosensory areas during motor preparation (Chatrian et al., 1959; Cuevas, Cannon, Yoo, & Fox, 2014; Fox et al., 2016; Gastaut, 1952; Pfurtscheller & Aranibar, 1979; Pfurtscheller & Berghold, 1989), while ERS in the beta-band over right frontal areas of the scalp is strongly associated with motor inhibition (Buschman & Miller, 2007, 2009; Siegel, Donner, Oostenveld, Fries, & Engel, 2008). In contrast, phase-locked

electrophysiological responses found during movement anticipation such as the motor readiness cortical potential (MRCP) are unsuitable for measuring cortical activation and inhibition together (Shibasaki & Hallett, 2006).

The present experiment was motivated to test approach/avoidance accounts of the divergent effect of losses and gains on effortful performance using ERD measures. Approach/avoidance accounts of the divergent effect of losses and gains on effortful performance predict that gains should improve primary task performance in Go-primed trials, while losses improve primary task performance in NoGo-primed trials (Buzzell, Beatty, Paquette, Roberts, & McDonald, 2017; Hoofs, Carsten, Boehler, & Krebs, 2019; Houtman & Notebaert, 2013; Pratto & John, 1991). It would therefore be expected that negative incentives and NoGo motor-primes would induce avoidance behaviours, while positive incentives and Go motor-primes induce approach behaviours, and that losses would increase the effect of NoGo motor-primes, while gains increase the effect of Go motor-primes. As ERD measures have been used to reflect approach/avoidance motor expectations during a Go/NoGo task (Liebrand, Pein, Tzvi, & Krämer, 2017), these were predicted to reflect the approach/avoidance associations made with incentives and motor-primes.

It was hypothesised that frontal and posterior-parietal ERD in the alpha band, as well as bilateral sensorimotor ERD in the beta band, would be strongest when gains were anticipated and when Go-cues were likely to occur, and weakest when losses were anticipated and when NoGo cues were likely to occur. Interactions between approach/avoidance motor sets and incentive types were predicted to be revealed as losses sharpening the effect of inhibitory motor sets on ERD responses and gains sharpening the effect of approach motor sets on ERD responses. We further hypothesised that monetary losses would be more motivating than gains in the COGED

task and improve the NoGo stopping rate. However, losses were predicted to slow RTs relative to gains and that individual SVs of effort would be associated with reward- and motor-set related cortical activation patterns.

6.3 Methods

6.3.1 Participants

27 subjects (15 females) were recruited. However, 3 subjects were removed from subsequent anaylsis because of excessive muscle artefacts in the EEG data. The final sample included 24 subjects (14 females), aged 24.25 ± 6.24 (mean ± SD). The procedure used was approved by the Research Ethics Committee of the University of Liverpool, and all participants gave fully informed written consent at the start of the experiment, in accordance with the Declaration of Helsinki.

6.3.2 Procedure

The participants were first required to complete a cued Go/NoGo task, which was a modified version of the sustained vigilance task used previously (Byrne et al., 2020; Massar et al. 2016) and the cued Go/NoGo task used by others (Filipovic et al., 2000; Randall & Smith, 2011). Participants were then required to complete the discounting task described previously, with gain and loss trials included (Byrne, et al., submitted; Maasar 2016; Westbrook 2014). The trial structure of the tasks used can be seen in Figure 6.1.

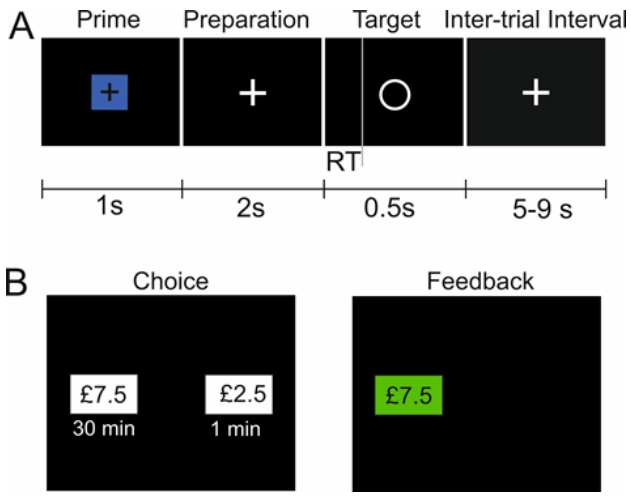

Figure 6.1 (A) A schematic representation of trials presented during the Go/NoGo task. The prime stimulus is shown to the left, sided by the anticipation period, the target stimulus, and the inter-trial interval (B) A schematic representation of the discounting task, with an example choice followed by a feedback period, confirming the selected option.

The Go/NoGo task consisted of four twenty-minute blocks, with 120 trials each. The reward and prime conditions were psuedo-randomly rearranged within each set of trials, meaning there was an equal number of trials for each incentive and reward trial within each block. In the gain condition, participants were offered a small monetary reward (+10p) whenever they reacted faster than their median RT in response to a Go cue, or successfully inhibited their response to a NoGo cue. In contrast, in the loss conditions, participants lost a small amount of money (-10p) whenever they reacted slower than their median RT in response to a Go' cue, or if they failed to inhibit their response to a NoGo cue, and in the 0p condition participants were not offered a reward.

Additionally, participants were primed to expect a Go or NoGo cue. When participants were primed for a Go cue, they were told there was a 75% chance of the following target being a Go cue and a 25% chance of it being a NoGo cue; and when participants were primed for a NoGo cue, they were told that there was a 75% chance of the following target being a NoGo cue and a 25% chance of it being a Go cue.

The effect of the different monetary incentives and primes on effortful performance and corresponding cortical responses were assessed using participants' mean RTs and electrophysiologically using their changes in ERD in the 2s epoch preceding the presentation of the target stimulus. RTs and other measures of effortful performance have been used in previous studies as measures of effortful engagement (Aarts et al., 2008; Atkinson & Raynor, 1978; Bandura & Cervone, 1983; Eisenberger, 1992; Kukla, 1972; Locke & Latham, 1990; Wang et al., 2021; Luft et al., 2009), and have been associated with physiological measures of effortful engagement such as pupil diameter (Massar, Lim, Sasmita, & Chee, 2016). However, ERD measures, reflecting the involvement of task-relevant cortical regions, are required to shed further light on the gap between effortful engagement and effortful performance under differing incentives and task conditions.

The discounting task was the same as used previously (Byrne, et al., submitted), being a modified version of the COGED task (Massar et al., 2016; Westbrook et al., 2013), with monetary losses added. Discounting procedures allowed us to estimate the subjective value (SV) of different levels of effort in equivalent loss and gain modalities.

6.3.3 Go/NoGo task

Once the EEG net was applied, participants were taken into a dimly lit, sound-attenuated room and asked to complete the Go/NoGo task. The Go/NoGo task was a combination of the cued vigilance task used previously (Byrne et al, 2020), and the cued (S1-S2) Go/NoGo tasks (Filipovic et al., 2000; Randall & Smith, 2011).

During the baseline period, participants were presented with a white cross and not required to make a response. The participants were then presented with a cue stimulus which displayed the reward or punishment offered for that trial (-10p, 0p,

+10p), as well as the probability of the target being a Go or a NoGo cue (75% Go, 75% NoGo), as indicated by the colour of the cue stimulus (blue, purple). After two seconds the participants were presented with the target stimulus (Go, NoGo). The inter-trial interval between the target stimulus and the baseline period was uniformly distributed and ranged from 3 to 7 seconds (see Figure. 6.1A).

Participants were instructed to respond as quickly as possible upon the occurrence of the Go stimulus and not make any response when presented with the NoGo stimulus. Participants were also informed of the probabilities of a Go/NoGo trial associated with each colour at the beginning of the experiment, which was kept consistent across each individual participant and counterbalanced across participants. The Go/NoGo target stimulus could be either a white circle or a white square, the associations with these targets was randomly assigned at the start of the experiment for each participant (e.g., a circle for Go and a square for NoGo). The participants were informed of this assignment before they began the task.

Participants completed a 15-trial practice run, with no rewards offered, allowing them to familiarise themselves with the rules of the task. Their median RT was calculated from this practice block and recalculated following each trial during the experimental blocks.

Participants were then required to complete four experimental blocks, lasting roughly twenty minutes, with 120 trials per block, and they completed 160 trials for each reward condition (-10p, 0p, +10p), with 80 Go primed trials and 80 NoGo primed trials. Participants were offered a maximum total gain/loss of £16 if they earned the reward or failed to avoid the loss on every trial. As the order of trials was pseudo-randomly rearranged at the start of each set of 5 trials, there was an equal number of trials for each condition and participants could not predict the next trial.

6.3.4 Discounting task.

Once the participants had completed the Go/NoGo task, they engaged in the discounting task (Massar et al., 2016; Westbrook et al., 2013), which was the same task as used previously (Byrne et al., submitted). The subjective cost of different levels of cognitive effort in both gain and loss conditions was evaluated by calculating the indifference point, defined as the average of the largest amount for which the participant chose the low-effort option and the smallest amount for which the participant chose the high-effort option. The indifference point represented the point that the subject perceived the high- and low-effort options as being subjectively equal, or changed their response from their initial choice. The area under the curve (AuC) in the participants SVs across effort levels was computed (Myerson, Green, & Warusawitharana, 2001), a measure which has been found to correlate with need for cognition scores (Westbrook et al., 2013). Bivariate correlations were conducted to assess the relationship between individual AuCs and their RTs and ERD results.

In this task, participants chose between two monetary gains (up to £12), or two monetary losses (up to £12), and each choice was between one lower monetary offer and one higher monetary offer (Figure 6.1). The monetary choices were tied to two effort-based outcomes, with one low-effort outcome (completing the task again for 1 minute) and one high-effort outcome (completing the task again for 5, 10, 15, 20, 25, or 30 minutes). In gain choices, the lower-monetary incentive was always tied to the low-effort outcome and the higher-monetary incentive was always tied to the high-effort outcome. In loss choices, the higher monetary loss was always tied to the low-effort outcome and the lower monetary loss was always tied to the high-effort option.

After each choice, the monetary reward/loss for each pair of offers was adjusted following a staircase titration method (i.e., in gain conditions, the low-effort

option was increased if the high-effort option was chosen and decreased if the low-effort option was chosen), and the amount of money being added to, or taken away from, the choices was halved each time the participants made a choice. Once, the participant had completed the task, one trial was randomly selected, and the participant was required to complete the Go/NoGo for the chosen amount of time and would receive the monetary gain/loss tied to that choice. The participants were made aware of the time they would have to complete the Go/NoGo task again, and its associated monetary outcome once the discounting task was completed.

The indifference point has been used by previous researchers as a measure of individual effort-discounting rates based on participant's willingness to engage in an effortful task for longer periods of time (Massar et al., 2016; Westbrook et al., 2013) and significantly correlates with the need for cognition score (Westbrook 2013). Providing further support for the validity of COGED indifferent point measures, the discounting curve taken from COGED tasks commonly matches the sigmoidal shape associated with effort discounting (Massar et al., 2016; Klein-Flügge et al., 2015).

However, while it is clear that prolonged engagement with tasks requiring sustained vigilance is perceived as effortful (Warm et al., 1996), the choices made to engage in effortful tasks for prolonged periods of time may employ different cognitive processes to the choice to maintain engagement during ongoing effortful engagement. Bivariate correlations were therefore conducted to assess the relationship between individual AuCs and RT/ERD results.

To control for temporal discounting, participants were informed that they would be required to remain in the laboratory for the full 30 minutes in total, including the time spent completing the task; ensuring that the participants made decisions during the discounting task based upon the effort required, rather than the time taken

to complete the task. While the effect of boredom associated with remaining in the lab was not directly investigated, all participants discounted higher levels of effort (30 mins) more than lower levels of effort (5 mins), suggesting that they were all reluctant to complete the task for longer periods of time.

6.3.5 EEG recordings.

The EEG net was aligned with reference to two preauricular points and the nasion landmark. Data was then recorded continuously using a 129-channel Geodesics EGI system (Electrical Geodesics, Inc., Eugene, Oregon, USA) with a sponge-based HydroCel Sensor Net. Electrode-to-skin impedances were kept below 50 kΩ and kept at equal levels across all electrodes, a recording band-pass filter was set at 0.001-200 Hz with a sampling rate of 1000 Hz, and the Cz electrode was used as a reference electrode.

6.3.6 Spectral analysis of EEG signals.

EEG data was then pre-processed using BESA v 7.0 (MEGIS GmbH, Germany), and re-referenced using a common average reference method (Lehmann, 1984), restoring the signal at electrode Cz.

Next, a principal component analysis method (Berg and Scherg 1994) was used to remove eye-blinks and electrocardiographic artefacts and data was visually inspected for muscle artefacts; all trials containing artefacts were excluded from subsequent analysis.

The average number of trials accepted for EEG analysis in each Go primed condition was: 65.5 ± 10.19 (mean ± SD) in the -10p condition; 65.67 ± 10.11 (mean ± SD) in the 0p condition; 65.58 ± 8.79 (mean ± SD) in the +10p condition, and in each NoGo primed condition was: 67.25 ± 8.14 (mean ± SD) in the -10p condition;

66.63 ± 10.51 (mean ± SD) in the 0p condition; 67.25 ± 8.14 (mean ± SD) in the +10p condition. The mean number of accepted trials did not differ across reward conditions ($p > .05$); however, significantly more NoGo cued trials were accepted than Go cued trials ($p = .034$), possibly due to greater muscle activity as a result of motor preparation in Go cued trials.

6.3.7 Event-related desynchronization analysis

To compute the ERD curves, EEG signals were down sampled to 256 Hz. Power spectra was computed in Matlab R2020a (The Mathworks, Inc., USA) using Welch's power spectral estimate method. All epochs comprising one set of epochs were aligned to form a quasi-continuous EEG signal. The power spectral densities were computed from non-overlapping 1-second segments (256 points), which were smoothed using a Hanning window, and were estimated in the range 1-80 Hz with a frequency resolution of 1 Hz.

ERD curves were evaluated from 2 s before, and 5 s after the onset of the cue stimulus in both the alpha (8-12 Hz) and beta (16-24 Hz) bands using the classical ERD transformation (Pfurtscheller & Aranibar, 1979). Absolute band power was calculated from 1 s time epochs shifted in 100 ms across the 7 s time window. The baseline used in the ERD calculation was the epoch ranging from -1.5 s to -0.5 s before the onset of the cue stimulus, and the time-epoch ranging from 2 to 3 s after the onset of the cue stimulus was chosen for statistical analysis.

6.3.8 Statistical analysis.

The main effects and interactions between reward and primes on median RTs and NoGo error rates were assed using 2×3 repeated measures ANOVAs with three levels of reward (-10p, 0p, +10p), and two-levels of prime (75% Go, 75% NoGo). To

test the assumption of normality used in the ANOVA a Shapiro-Wilk test of normality was used. The test was chosen above that of Kolmogorov-Smirnov because it was more appropriate for the small sample size used (Guo, 2012; Zimmerman, 2003). NoGo stopping rates were defined as the percentage number of trials where participants successfully inhibited their response to NoGo cues in each reward/prime condition.

Similarly, ERD changes due to reward and primes were investigated in both the alpha (8-12 Hz) and beta (16-24 Hz) frequency bands across all 129 electrodes using 2×3 repeated measures ANOVAs. However, to correct for false positive errors due to repeated significance tests, p values were calculated for each electrode using a permutation analysis (Maris & Oostenveld, 2007), implemented in the *Statcond.m* program in the EEGLab 2019 package (Makeig, Debener, Onton, & Delorme, 2004). Then, to ensure that only electrodes with a significantly large ERD or ERS were included in subsequent analysis, T-tests with significance thresholds of $p = .01$ were used to test whether ERD values over each electrode were significantly different from 0. Electrode clusters showing significant effects in both the permutation analysis and the t-tests were selected for further investigation in the 2×3 repeated measures ANOVAs using SPSS v.22 (IBM Inc., USA), and a Greenhouse-Geisser epsilon correction was used to tackle violations of sphericity in the data.

The AuC (Myerson et al., 2001) in the indifference points across effort-levels in the discounting task was computed for every participant. The AuC has previously been found to be correlated with need for cognition scores (Westbrook et al., 2013), and was used as an estimate as individual SVs of effort in terms of monetary gains and losses separately (Byrne, et al., submitted).

Pearson's correlation coefficients between individual RTs, changes in ERD, and the AuC of SVs in the discounting task were computed to test for possible associations between behavioural data and ERD.

6.4 Results

6.4.1 Go/NoGo Task

RT data was tested for normality using a Shapiro-Wilk test, finding that the data did not significantly deviate from normality (W = .93, p = .082). Median RTs were therefore assessed using parametric testing. Differences between median RTs were compared across the two prime conditions (Go, NoGo) and three reward conditions (-10p, 0p, +10p) using a 2×3 repeated measures ANOVA. A significant main effect of prime was found ($F(1,23) = 21.48$, $p < .001$, $\boldsymbol{\eta p^2} = .48$), with RTs in Go primed trials being significantly faster than those in NoGo primed trials.

A significant main effect of reward was also found ($F(2,46 = 17.02$, $p < .001$, $\boldsymbol{\eta p^2} = .43$). Further analysis of the data revealed this main effect to be due to RTs in the +10p condition being significantly faster than in both the 0p condition ($p < .001$), and in the -10p condition ($p = .004$). RTs in the -10p condition were also significantly faster than those in the 0p condition ($p = .005$). However, no significant interaction was found between prime and reward conditions ($p > .05$), suggesting that prime and reward effects acted independently.

Differences between percentage error rates in NoGo trials were also compared, and a significant main effect of prime was found ($F(1,23) = 45.36$, $p < .001$, $\boldsymbol{\eta p^2} = .664$), with percentage error rates in NoGo primed trials being much lower than those in Go primed trials. A significant main effect of reward was also found ($F(2, 46) = 3.86$, $p = .043$, $\boldsymbol{\eta p^2} = .14$), and further analysis showed that this effect resulted from

the NoGo stopping rate being lower in the +10p reward condition than in the 0p reward condition, meaning participants made more incorrect responses to NoGo cues in gain compared to no incentive conditions.

Finally, differences between percentage Go-success rates were compared using a 2×3 repeated measures ANOVA. This analysis revealed significant main effects of both the prime ($F(1,23) = 101.02$, $p < .001$, $\eta p^2 = .82$) and reward ($F(2,46) = 36.26$, $p < .001$, $\eta p^2 = .62$) and a statistically significant interaction between reward and prime ($F(2,46) = 16.18$, $p < .001$, $\eta p^2 = .41$). The main effect of prime was due to Go-success rates being significantly higher in Go-primed trials compared to NoGo-primed trials, and the main effect of reward was due to Go-success rates being significantly better in no-incentive trials compared to gain ($p < .001$) or loss ($p < .001$) trials, and in gain compared to loss trials ($p = .002$). The interaction between reward and Go/NoGo prime was found to be due to the significant difference between Go- and NoGo-primed trials in gain and loss, but not in no incentive conditions. The significant interaction found may be indicative of a ceiling effect in no incentive trials.

A bar chart showing the RTs across reward and prime conditions can be seen in Figure 6.2A, a bar chart showing NoGo stopping rates across reward and prime conditions can be seen in Figure 6.2B, and a bar chart showing Go success rates across reward and prime conditions can be seen in Figure 6.2C. Go-success rates across reward and prime conditions can be seen in Figure 2C.

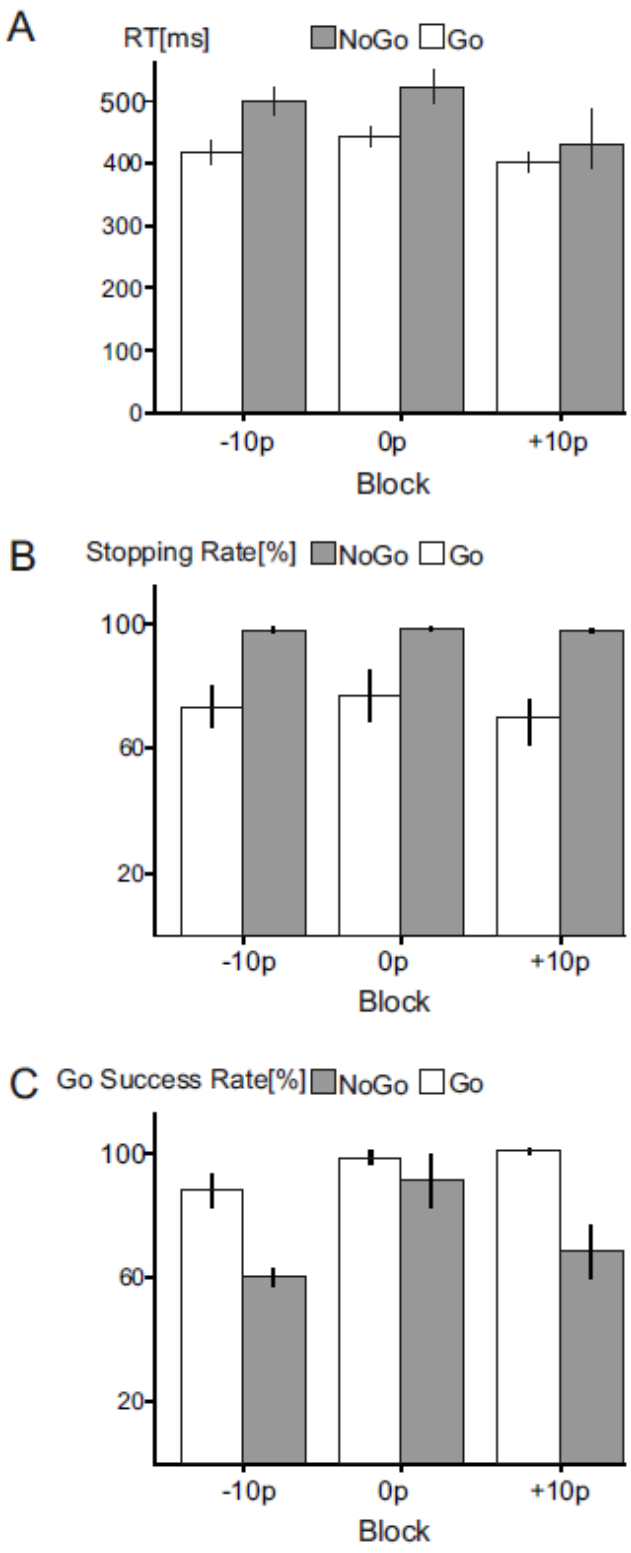

Figure 6.2. A bar chart showing median RTs in response to go stimuli for each reward condition (-10p, 0p, +10p) (A). A bar chart to show percentage stopping rates in response to NoGo stimuli for each reward condition (B). White bars show RTs and stopping rates for NoGo primed trials and grey bars show Go trials. Error bars represent the standard errors of the mean.

6.4.2 Discounting task

A 6×2 ANOVA was conducted to compare the main effects of effort level (5, 10, 15, 20, 25, 30 minutes) and gain/loss condition (gains, losses) on the participant indifference points. The discounting curve shown from the choice task is shown in figure 6.3. A significant main effect of effort level was found ($F(5,120) = 28.27$, $p = .001$, $\boldsymbol{\eta p^2} = .55$), with a significant linear trend ($p < .001$). There was a significant difference between all effort levels ($p < .05$), meaning that participants were more likely to choose the low-reward option in high effort trials. . A significant main effect of gain/loss conditions was also found, with indifference points in loss trials having a significantly larger AuC than gain trials ($F(1,24) = 6.28$, $p = .044$, $\boldsymbol{\eta p^2} = .16$) , indicating that monetary losses were significantly more motivating than equivalent gains.

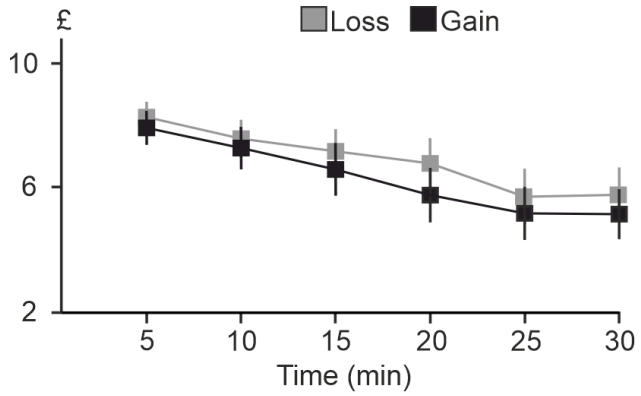

Figure 6.3. A line graph to show the discounting curve in the choice task, with the mean subjective value shown for each block in the task (5, 10, 15, 20, 25, 30 minutes). Error bars represent standard errors of the mean.

The associations between the subjective value of effort, evaluated as AuC of the discounting curve, in gain and loss conditions and ERD/ RT changes under gain and loss trials were evaluated using bivariate correlations. Specifically, individual subjective values of effort for loss- and gain-conditions in the discounting task were

compared with ERD in gain and loss trials in the Go/NoGo task. To compare individual sensitivities to gain and loss conditions in both subjective value of effort and ERD and RTs , a difference variable was computed representing the AuC of individual discounting rates in gain conditions subtracted from the AuC of individual discounting rates in loss conditions. Similarly, difference variables were created for ERD and RTs, defined as the ERD or RT values found in gain trials subtracted from values found in loss trials. However, no statistically significant correlations were found ($p > .05$) between gain/loss AuC findings and ERD or RT changes in gain and loss trials.

6.4.3 ERD patterns across trials

The time courses and topographic maps of alpha, beta, and theta ERD/ERD for Go- and NoGo-primed trials are shown in Figures. 6.4A-C and 6.5A-C, respectively. Activity during the presentation of the cue stimulus (0.5 s after cue onset) were featured by a prominent alpha ERD (Figures. 6.4A and 6.5A) over occipital electrodes, which is thought to represent the attentional and visual processing of the stimulus cue. During period of motor preparation (2-2.5 s after cue onset), both alpha and beta-band ERD was found over motor and sensorimotor areas. ERD in the beta band (Figures. 6.4B and 6.5B) was comparatively weaker in this period and distributed mainly over contralateral regions compared to ERD in the alpha band, which occurred over more posterior electrodes when compared to beta-band ERD. During the period of response execution or suppression (3.3 s after cue onset), ERD was observed bilaterally in both frequency bands, which occurred over more posterior regions in the alpha-band than in the beta-band. ERD patterns in both the alpha and beta bands showed a similar pattern in both Go- and NoGo-primed trials, with weaker ERD shown in NoGo-primed trials.

Finally, in the theta band (Figure. 6.4C and 6.5C), ERD/ERS during the cue interval (0.5s after cue onset) was confounded by phase-locked evoked responses, causing a large ERS over the entire scalp. The following periods were featured by a theta ERS over central and precentral midline electrodes which grew stronger as the participants anticipated the target stimulus.

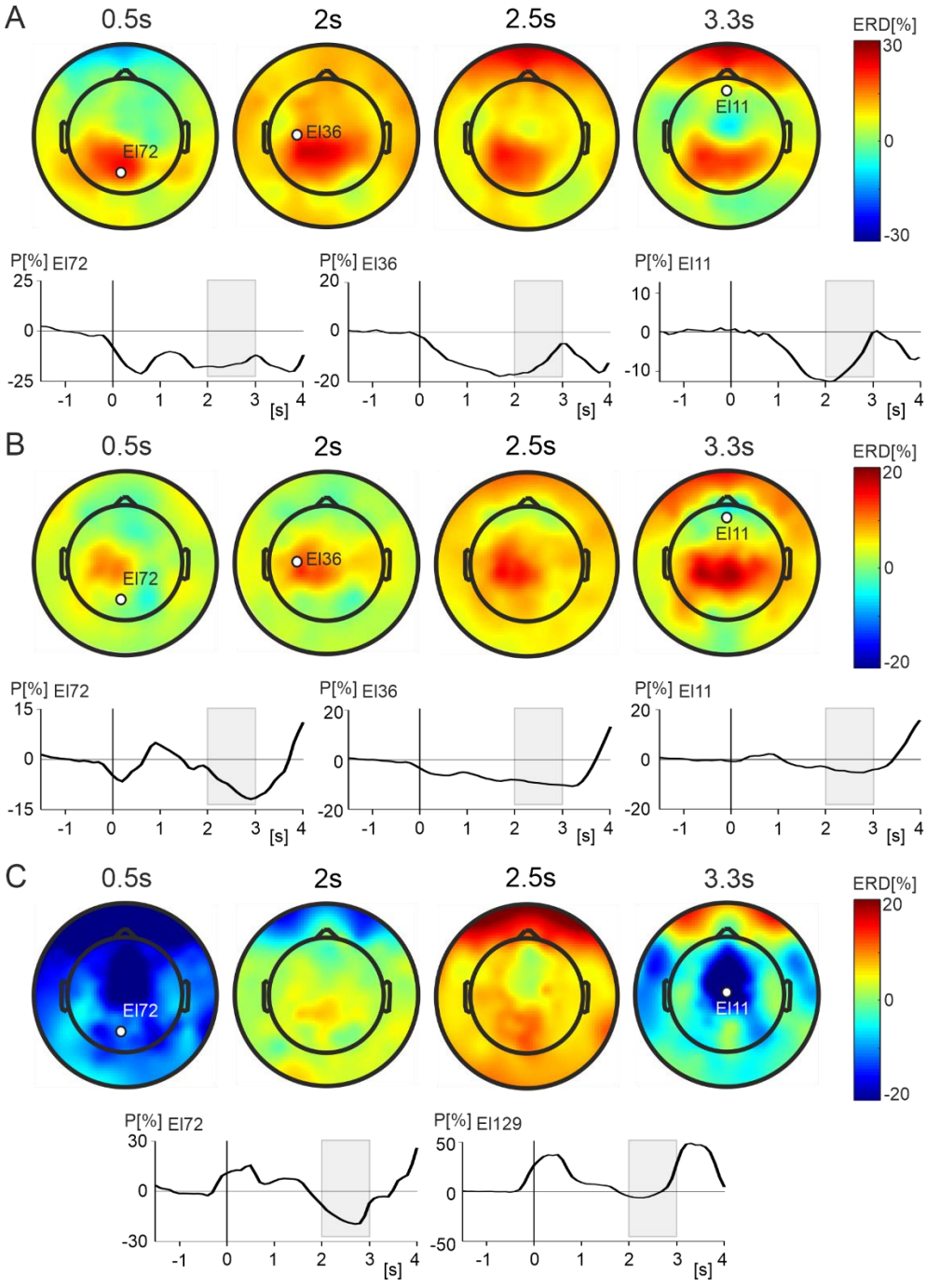

Figure 6.4. Topographic maps showing ERD in Go primed trials at four time points (top); first, during the presentation of the priming stimulus (0.5 s), then the early period of a 75% Go/NoGo anticipation (2 s), and the late period of a 75% Go/NoGo anticipation (3.3 s), second (bottom) % power changes at selected electrodes, with grey rectangles covering the interval from 2s to 3 s representing the epoch selected for further analysis. ERD results are shown for the alpha (A), beta (B), and theta (C) bands.

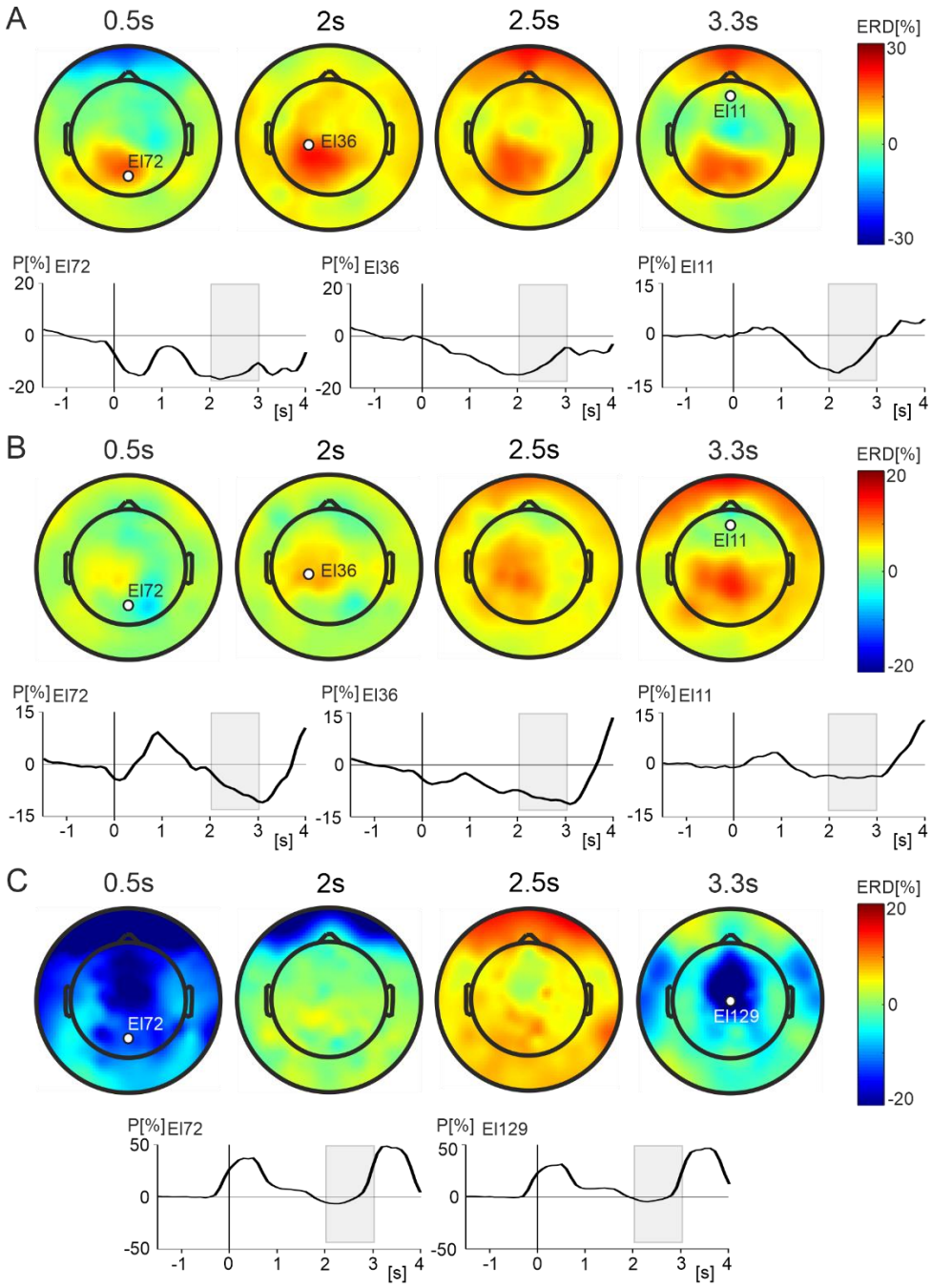

Figure 6.5. Topographic maps showing ERD in NoGo primed trials at four timepoints (top); first, during the presentation of the priming stimulus (0.5s), then the early period of a 75% Go/NoGo anticipation (2s), and the late period of a 75% Go/NoGo anticipation (3.3s), second (bottom) % power changes at selected electrodes, with grey rectangles covering the interval from 2 to 3s representing the epoch selected

for further analysis. The ERD maps and curved are shown for the alpha (A), beta (B), and theta (C) bands.

6.4.4 Alpha-band ERD

The grand average topographic maps showing alpha-band for all trials as well as the electrodes found to be significantly different from 0 are shown in Figure. 6.6A. Topographic maps showing ERD for Go primed trials in each of the three reward conditions are shown in Figure. 6.6B, and topographic maps showing ERD for NoGo primed trials are shown in Figure. 6.6C. ERD can be seen over contralateral sensorimotor areas in all conditions, becoming bilateral in Go primed trials and both gain and loss trials (+10p, -10p), and spreading to frontal electrodes when participants were incentivised with a gain or loss.

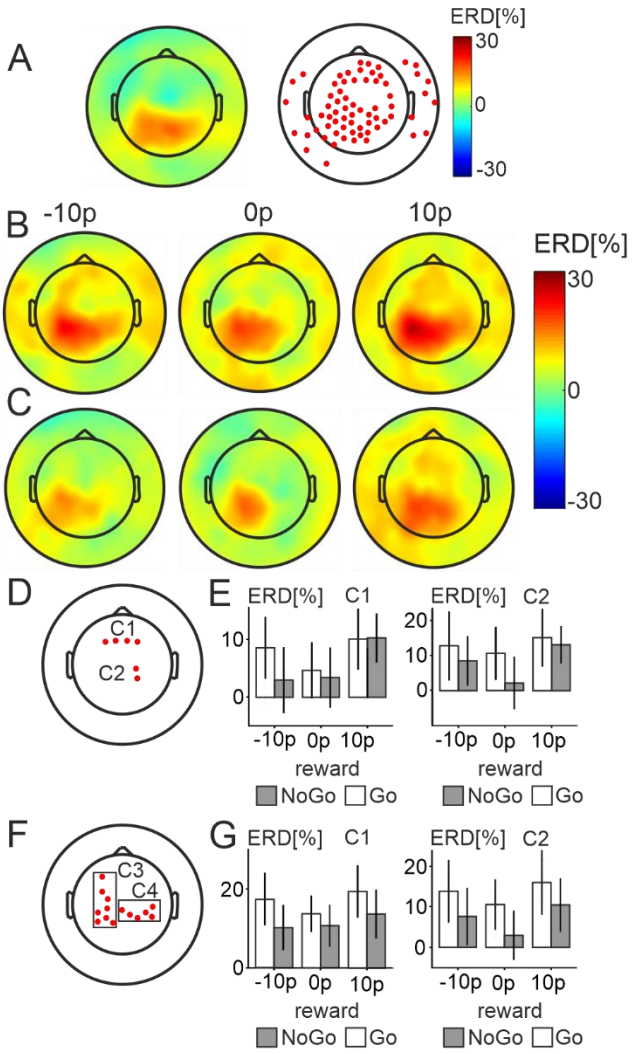

Figure 6.6. (A) A topographic map of alpha-band ERD across all conditions and trials (left), and electrodes showing a prominent alpha-band ERD across all conditions (right). (B) Topographic maps of alpha-band ERD in three reward conditions during Go-primed ERD trials and (C) NoGo-primed trials. (D) Location of electrodes in two clusters manifesting statistically significant effect of reward, with (E) bar charts showing mean alpha-band ERD each of three reward conditions in NoGo-primed (grey rectangles) and Go-primed (white rectangles) trials. Error bars represent standard error of the mean. Location of electrodes in two clusters manifesting statistically significant effect of prime (F), with (G) bar charts showing mean alpha-band ERD each of three reward conditions in NoGo-primed (grey rectangles) and Go-primed (white rectangles) trials. Error bars represent standard error of the mean.

To investigate the effects of reward and prime on ERD values, 2×3 repeated measures ANOVAs were computed to assess using prime (75% Go, 75% No-Go) and reward (-10p, 0p, +10p) as factors. ERD values were only analysed over electrode

clusters which passed the combined statistical and amplitude thresholds (Figure. 6.6A), ensuring that only electrodes showing a robust ERD across conditions were assessed.

The 2×3 repeated measures ANOVA revealed two clusters showing a main effect of reward; one in central-frontal regions of the scalp (C1) and one over the ipsilateral posterior parietal region (C2). The locations of these electrode clusters are shown in Figure. 6.6D. The statistically significant main effect of reward in the frontal cluster of electrodes ($F(2,46) = 6.43$, $p = .003$, $\boldsymbol{\eta p^2} = .22$) was the result of the ERD in the +10p reward conditions being stronger than that in both the 0p ($p = .002$) and -10p ($p = .02$) conditions, with a significant quadratic trend ($p = .002$). In contrast, significant main effects of both reward ($F(2,46) = 5.16$, $p = .01$, $\boldsymbol{\eta p^2} = .18$) and prime ($F(1,23) = 6.23$, $p = .02$, $\boldsymbol{\eta p^2} = .21$) were found over the posterior parietal cluster of electrodes (C2). The main effect of reward was due to the ERD in +10p reward trials being significantly stronger than in 0p reward trials ($p = .01$), with a significant quadratic trend found ($p = .01$), and the main effect of prime was the result of ERD being stronger in Go primed conditions compared to NoGo primed conditions. Bar charts showing the ERD differences in these clusters is shown in Figure 6.6E.

The 2×3 repeated measures ANOVA found two clusters of electrodes to have significant main effects of prime; one over the contralateral posterior parietal cortex, moving anteriorly to sensorimotor areas, and one over the ipsilateral posterior parietal cortex (Figure. 6.6F). A statistically significant main effects of and prime was found over the contralateral cluster (C3) of electrodes ($F(1,23) = 14.74$, $p = .001$, $\boldsymbol{\eta p^2} = .39$), and this was due to the ERD in Go primed trials being stronger than in NoGo primed trials. Similarly, a significant main effects of prime ($F(1,23) = 12.14$, $p = .002$, $\boldsymbol{\eta p^2} = .35$) were found in the ipsilateral cluster of electrodes (C4), with this being due to ERD

in the Go primed condition being stronger than in the NoGo primed condition. No significant interaction between reward or prime were found in any of the electrode clusters selected for further analysis. Bar charts showing ERD values across conditions can be seen in Figure. 6.6G.

To analyse the correlations between behavioural and ERD results, difference variables were created by subtracting individual NoGo primed RTs and ERD values from Go primed RTs and ERD values, as well as subtracting individual ERD and RT values in the 0p and the -10p conditions from those in the +10p condition. However, no significant correlations were found, between ERD and RT difference variables, or between ERD difference variables and individual AuC rates in the COGED task.

6.4.5 Beta-band ERD

The grand average topographic map for all trials and the distribution of electrodes showing an ERD significantly different from zero are shown in Figure. 6.7A. Activity in the beta-band was charecterised by a consistent ERD over contralateral sensorimotor regions, an effect which became stronger and more bilateral in Go primed trials and when participants were offered a +10p reward. Grand average topographic maps in each of the three reward conditions are shown for Go primed trials in Figure. 6.7B and for No-Go primed trials in Figure. 6.7C.

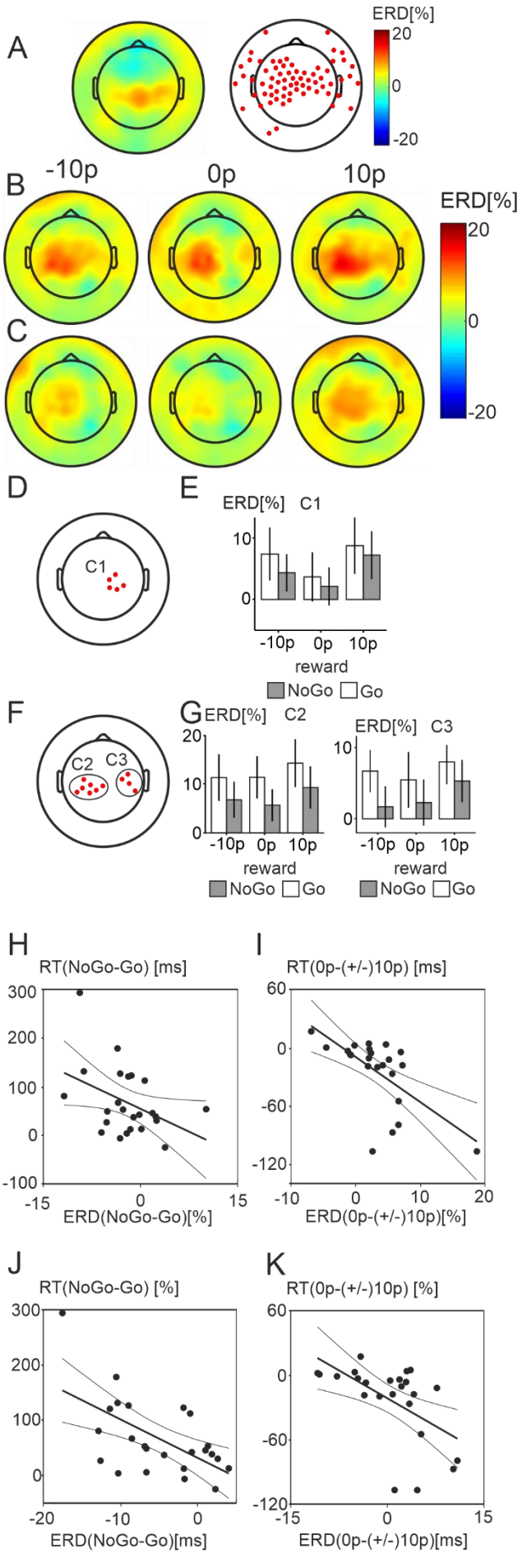
A
ERD[%]
20
0
-20
B
-10p
0p
10p
ERD[%]
20
0
-20
C
D
C1
E
ERD[%] C1
10
0
-10p 0p 10p
reward
NoGo Go
F
C2 C3
G
ERD[%] C2
20
10
0
-10p 0p 10p
reward
NoGo Go
ERD[%] C3
10
0
-10p 0p 10p
reward
NoGo Go
H
RT(NoGo-Go) [ms]
300
200
100
0
-100
-15 0 15
ERD(NoGo-Go)[%]
I
RT(0p-(+/-)10p) [ms]
60
0
-60
-120
-10 0 10 20
ERD(0p-(+/-)10p)[%]
J
RT(NoGo-Go) [%]
300
200
100
0
-20 -10 0
ERD(NoGo-Go)[ms]
K
RT(0p-(+/-)10p) [%]
60
0
-60
-120
-15 0 15
ERD(0p-(+/-)10p)[ms]

Figure 6.7. (A) A topographic map of beta-band ERD across all conditions and trials (left), and electrodes showing a prominent beta-band ERD across all conditions (right). (B) Topographic maps of alpha-band ERD in three reward conditions during Go-primed ERD trials and (C) NoGo-primed trials. (D) Location of electrodes in two clusters manifesting statistically significant effect of reward, with (E) bar charts showing mean alpha-band ERD each of three reward conditions in NoGo-primed (grey rectangles) and Go-primed (white rectangles) trials. Error bars represent standard error of the mean. Location of electrodes in two clusters manifesting statistically significant effect of prime (F), with (G) bar charts showing mean alpha-band ERD each of three reward conditions in NoGo-primed (grey rectangles) and Go-primed (white rectangles) trials. Error bars represent standard error of the mean. Scatter plots showing the correlation between RT and ERD difference variables calculated between Go and NoGo trials (NoGo-Go) for cluster 1 (H) and cluster 3 (I), and scatter plots showing the correlation between RT and ERD difference variables calculated between no incentive and incentive trials (0p – (-10p + +10p)) for cluster 1 (H) and cluster 3 (J).

Three clusters of electrodes showing a significant main effect of reward or prime were found in the left (contralateral) and right (ipsilateral) sensorimotor region of the scalp. Consistent with previous research (Salmelin & Hari, 1994; Stancak & Pfurtscheller, 1996), these clusters were marginally more anterior than the cluster of electrodes selected in the alpha band (Figures 6.6B-C).

The significant main effect of reward found in the ipsilateral sensorimotor cluster of electrodes (C1;shown in Figure 6.7D) ($F(2,46) = 11.73$, $p < .001$, $\eta p^2 = .34$) was found to be the result of ERD in the 0p reward condition being significantly weaker than in both the +10p condition ($p < .001$) and the -10p condition ($p = .01$), but no difference was found between the +10p and -10p conditions ($p > .05$). A significant main effect of prime was also found in this cluster of electrodes ($F(1,23) = 4.65$, $p = .042$, $\eta p^2 = .17$), with ERD being stronger in Go primed compared to NoGo primed trials. A bar chart to show the ERD across conditions for this cluster can be seen in Figure 6.7E.

Two clusters were found in the permutation analysis with significant main effects of prime. The locations of these clusters are shown in Figure. 6.7F. The first

cluster (C2), was found over contralateral sensorimotor regions, and the main effect of prime ($F(1,23) = 17.30$, $p < .001$, $\eta p^2 = .43$) was due to ERD in Go primed trials being stronger than in NoGo primed trials. The second cluster (C3) was found over ipsilateral sensorimotor area, where the main effect of prime ($F(1,23) = 17.08$, $p < .001$, $\eta p^2 = .43$) was the result of a stronger ERD in Go primed compared to NoGo primed trials. No significant interactions were found between reward and prime in any of the electrode clusters selected for further analysis. Bar charts of ERD values across conditions in these two clusters can be seen in Figure. 6.7G.

To test the relationship between ERD changes in the beta band and RT changes, difference variables were created by subtracting Go primed from NoGo primed ERD and RTs, as well as by subtracting mean ERD and RTs in the +10p and -10p conditions from those in the 0p condition.

Two significant correlations were found between RTs and ERD difference variables in the right-central cluster of electrodes (C1). First, a significant negative correlation was found ($r = -.41$, $p = .046$) between the prime difference variables (NoGo primed trials subtracted from Go primed trials; see Figure. 6.7H) calculated between individual RTs and ERD values. The correlation indicates that participants who showed faster RTs in Go- compared to NoGo-primed trials also showed stronger ERD in Go compared to NoGo-primed trials. Second, a significant negative correlation ($r = -.65$, $p = .001$) was found between the RT and ERD difference variables calculated between the +10/-10 p conditions and the 0p condition (+10/-10 p subtracted from 0 p) (Figure 6.7I-H) in this cluster. The second correlation shows that participants who displayed shortening of RTs to positive/negative incentives compared to no incentive conditions also showed stronger ERD in gain/loss trials compared to no incentive trials.

Two statistically significant negative correlations were also found in the left-central cluster of electrodes (C2). One correlation was found between the difference variables calculated between the Go and NoGo primed conditions for RTs and ERD changes (r = -.59, p = .002; see Figure 6.7J), showing that participants who displayed faster RTs in Go-primed compared to NoGo-primed conditions also showed stronger ERD in Go-primed relative to NoGo-primed trials. The other correlation was found between the difference variables calculated between the +10/- 10 p conditions and the 0 p condition (+10/-10 p subtracted from 0 p) (r = -.53, p = .003; see Figure 6.7J). This correlation indicates that participants who responded more quickly to the Go cue in positive/negative relative to no incentive conditions also showed stronger beta-band ERD in these conditions compared to during no incentive trials.

6.4.6 Interactions between frequency and reward/motor-prime

To analyse if alpha and beta bands were differently involved in effects of reward, prime or their interaction, three-way ANOVAs involving factors of frequency bands (alpha vs. beta), reward (+10p, 0p, -10p) and motor cue (Go vs. NoGo) were carried out in clusters of electrodes showing statistically significant effects of reward or primes in both frequency bands. These analyses revealed that an electrode located in ipsilateral central region of the scalp overlying the sensorimotor cortex (electrode 83, Figure 6.8A & B) manifested a statistically significant interaction between frequency bands and Go/NoGo primes (F(1,23)= 10.451, p = .004, $\boldsymbol{\eta p^2}$= .312); this interaction was caused by a significantly larger ERD in NoGo than Go trials in the alpha band (p = .002) but not in beta band (p > .05).

Another electrode, also located in ipsilateral central region of the scalp (electrode 103, Figure 6.8 C and D), showed a statistically significant interaction between frequency bands and reward (F(2,46) = 4.54, p = .016, $\boldsymbol{\eta p^2}$ = .165). This

interaction was related to the presence of a statistically significant effect of reward in the alpha band (F(2,46) = 3.80, p = .032, ηp^2 = .142) but not in the beta-band (P > 0.05).

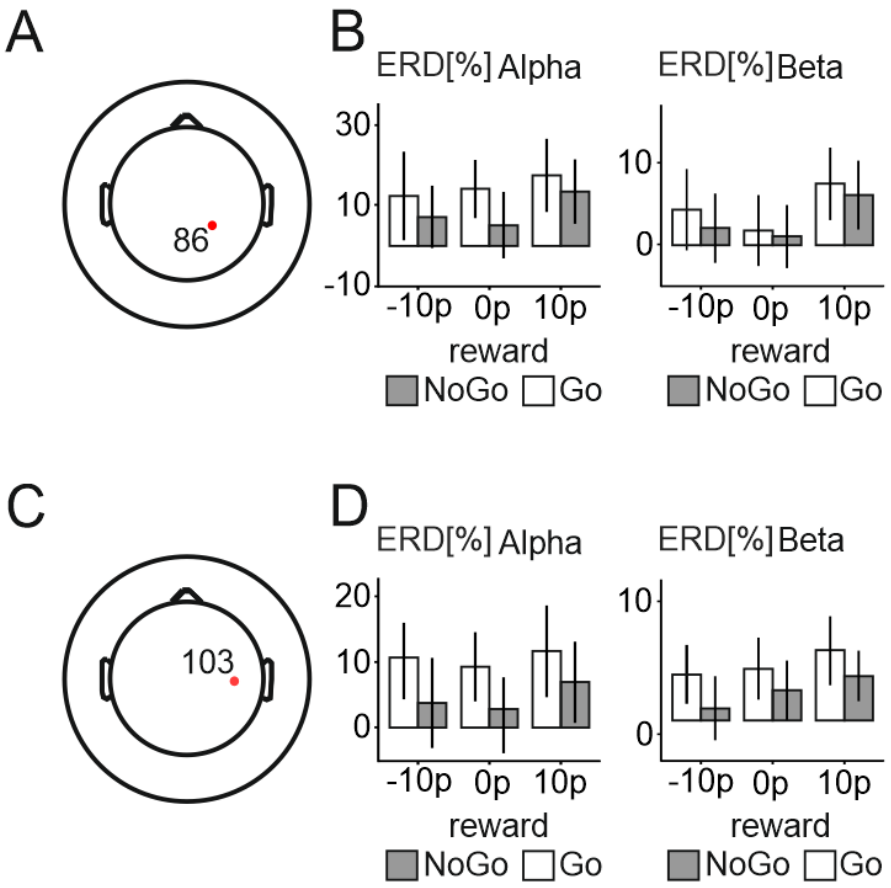

Figure 6.8. (A) Location of electrode 86, showing a significant interaction between frequency and prime, and (B) bar charts showing the mean alpha- and beta-band ERD in each of the three reward and two prime conditions in electrode 86. Error bars represent the standard error of the mean. (C) Location of electrode 103, showing a significant interaction between frequency and reward, and (D) bar charts showing the mean alpha- and beta-band ERD in each of the three reward and two prime conditions in electrode 86. Error bars represent the standard error of the mean.

6.5 Discussion

It was hypothesised that losses would be associated with the weakest alpha- and beta-band ERD prior to a speeded RT response when expecting a low probability of movement (NoGo cued), and that gains would be associated with the strongest ERD when expecting a high probability of movement (Go cued). While the results

confirmed the presence of a stronger alpha-band ERD in frontal and posterior-parietal scalp regions in gain compared to loss trials and in Go-cued compared to NoGo-cued trials, the effect of incentives and motor sets did not significantly interact. Further, although sensorimotor beta-band ERD was weaker in NoGo-primed conditions and no incentive trials, no difference was found between gain and loss conditions. The SV of effort, evaluated using a COGED method, was larger in loss than gain conditions but did not significantly correlate with ERD changes.

RTs were shorter in gain compared to loss trials, and alpha-band ERD was stronger over fronto- and posterior-parietal regions of the scalp in gain trials compared to loss and no incentive trials. In contrast, beta-band ERD over bilateral sensorimotor areas was sensitive to the presence of an incentive, but no difference was found between gain and loss conditions. Amplitude changes in cortical oscillations have previously been linked to value-based decision-making (Balconi, Finocchiaro, & Canavesio, 2014; Balconi & Mazza, 2009), and alpha oscillations have been shown to be subject to reward-learning in biofeedback paradigms (Byun & Hitchcock, 2012; Chatterjee, Aggarwal, Ramos, Acharya, & Thakor, 2007; Othmer, Othmer, & Kaiser, 1999; Sakamak, Tavakoli, Wiebe, & Adams, 2020). However, the beta-band ERD explored here likely refers to the state of motor preparation in the sensorimotor cortex (Kilner, Friston, & Frith, 2007; Miall, 2003; Palmer, Zapparoli, & Kilner, 2016; Filipović et al., 2001; Alegre et al., 2004; Liebrand et al., 2017 Liebrand et al., 2017), while fronto- and posterior-parietal alpha-band ERD may reflect the anticipatory attention in the fronto-parietal network required to quickly detect the upcoming target stimulus (Corbetta, Patel, & Shulman, 2008; Coull, Walsh, Frith, & Nobre, 2003; Kastner & Ungerleider, 2000; Serences & Yantis, 2006; Capotosto, Babiloni, Romani, & Corbetta 2009). Further, the patterns of NoGo stopping rates and Go-success rates

across incentive conditions indicates that the behavioural approach/avoidance effects of gains and losses on Go and NoGo behaviour found previously (Guitart-Masip et al., 2011; Guitart-Masip et al., 2012; Richter et al., 2014; Hoofs, Böhler, & Krebs, 2019) were replicated in the present experiment, although the improved Go-success rates in no incentive conditions suggests that gain and loss incentive cues may have distracted the participants from the primary task goals.

The patterns of ERD and RTs shown in response to gains and losses are consistent with our previous results comparing cortical oscillatory changes with reward (Byrne et al., submitted), although a previously unobserved preference for gains was revealed for RTs and alpha-band ERD. However, our previous research used a simple RT task, while in the present experiment participants were required to correctly identify a probabilistic Go/NoGo cue. Changes in anticipatory attention in loss compared to gain conditions as indicated by alpha band ERD may not have affected RTs found previously as no stimulus detection was required, meaning the attentional biases associated with gains and losses may be more pronounced in tasks requiring stimulus detection. The present results therefore suggest that anticipatory attention increased preferentially in response to gains over losses, aiding fast stimulus detection, while the motor preparation primarily employed in simple RT tasks increased with incentives, but was insensitive to their valence. The significant correlations between RT and beta-band ERD differences found across incentive and no incentive conditions support the idea that motor preparation drove the speeding of RTs under the presence of incentive but was insensitive to its valence. The results shown presently expand on the divergent effect of losses and gains on effortful performance (Carsten, Hoofs, Boehler, & Krebs, 2018; Fontanesi, Palminteri, & Lebreton, 2019; Paschke et al., 2015; Potts, 2011). The present results showed that

gains contributed to overall faster RTs through increased attentional engagement, while motor preparation contributed to faster responses motivated by the presence of an incentive, but did not account for differences found between gain and loss conditions.

While the patterns of effects of reward and primes were similar in alpha- and beta-bands across the clusters of electrodes, the electrodes overlying the ipsilateral sensorimotor cortex manifested stronger effects of reward and prime in the alpha- than beta-band. This finding may be related to an overall larger amplitude of band-power changes in the alpha- than beta band in ipsilateral sensorimotor cortex seen in previous studies involving voluntary movements (Niedermeyer, 2005; Pfurtscheller, Stancak, & Edlinger, 1997; Stancak & Pfurtscheller, 1996; Cuevas, Cannon, Yoo, & Fox, 2014; Fox et al., 2016).

Approach/avoidance motor sets were found to modulate similar patterns of ERD to monetary incentives. Alpha-band ERD over fronto- and posterior-parietal areas and beta-band ERD over sensorimotor areas were stronger when participants expected an approach (75% Go-cued trials) compared to an inhibitive response (75% NoGo-cued trials). Previous research investigating ERD changes during movement execution and inhibition has showed no difference in alpha-band ERD (Filipović, Jahanshahi, & Rothwell, 2001; Alegre et al., 2004), but a stronger beta-band ERD during the execution of Go compared to NoGo responses (Alegre et al., 2004). Expanding on these results, Liebrand, Pein, Tzvi, and Krämer (2017) showed significantly weaker anticipatory posterior alpha-band ERD, but stronger sensorimotor beta-band ERD, when participants expected the occurrence of a Go cue seconds later, compared to trials with equiprobable subsequent Go and NoGo cues. While the present findings of stronger alpha-band ERD during Go-primed trials seem at odds with those

found by Liebrand, Pein, Tzvi, and Krämer (2017), these differences can be reconciled by considering cue probability. Liebrand, Pein, Tzvi, and Krämer (2017) compared Go cues occurring with a 100% probability to equiprobable Go/NoGo trials, while the present study used Go/NoGo-primed conditions with equal probabilities of .75 of the occurrences of a subsequent Go/NoGo cue. The differences in Go/NoGo cue probabilities in Liebrand et al. (2017) and the present study may explain the differing results found rather than these being the result of Go/NoGo cue expectations. The 100% Go condition used by the researchers required no stimulus detection, which may have slowed RTs rather than approach/avoidance tendencies associated with Go/NoGo expectations. Taken with previous findings, the present results suggest that anticipatory alpha-band ERD is sensitive to attention or overall task engagement, while beta-band ERD is reflective of preparatory approach motor responses. The significant correlations found presently between differences in RTs and beta-band ERD across participants supports the hypothesis that sensorimotor beta-band ERD accounts for motor-approach behaviours, while alpha-band ERD reflects attention or task-engagement.

It has been posited that losses are associated with avoidance responses and gains with approach responses, and that the loss-avoidance response is stronger than the gain-approach response (Elliot, 2006; Phaf, Mohr, Rotteveel, & Wicherts, 2014; Solarz, 1960). It would therefore be expected that approach/avoidance motor sets would interact with losses and gains during effortful engagement; where losses sharpen the inhibitive effect of avoidance motor sets, while gains sharpen the activating effects of approach motor sets. However, while we found overlapping patterns of activation between incentive and approach/avoidance motor sets, no significant interactions were found between these variables. Early studies investigating

the interaction between incentive valence and approach/avoidance behavioural tendencies found that gains and losses enhance Go/NoGo performance in trials compatible to the valence of the offered incentive (i.e., Go-gain/NoGo-loss) (Guitart-Masip et al., 2011; Guitart-Masip et al., 2012; Richter et al., 2014; Hoofs, Böhler, & Krebs, 2019). A key methodological difference between previous studies investigating the interaction between approach/avoidance tendencies and incentive valence is whether the valence cue was presented seconds before the Go/NoGo target stimulus (Guitart-Masip et al., 2011; Guitart-Masip et al., 2012; Richter et al., 2014; Schevernels et al., 2016) or concurrent with the Go/NoGo stimulus (Boehler et al., 2012; Freeman et al., 2014), with the latter finding significant interactions between incentive valence and approach/avoidance tendencies. Task designs presenting incentive and target stimuli concurrently thereby tap into reactive control mechanisms, while those presenting incentive stimuli prior to the target stimulus tap into proactive control mechanisms (Krebs & Woldorff, 2017). Our data falls in line with the studies failing to show clear evidence of such incentive/action interactions (Boehler et al., 2012; Verbruggen & McLaren, 2018; Schevernels et al., 2016), suggesting that incentive valence modulates immediate approach/avoidance responses in reactive control mechanisms, but attentional biases associated with incentive valence modulate sustained proactive control mechanisms.

An important methodological difference which may partially account for the inconsistent interactions between approach/avoidance tendencies and incentive valence is whether the incentive is presented concurrent with the cue or the target stimulus. A more pronounced interaction between incentive valence and approach/avoidance responses occurs when target stimuli (Go/NoGo cues) are directly associated with incentives compared to when incentives are presented seconds before

(Hoofs, Böhler, & Krebs, 2019). The placement of incentive valence concurrent with target or cue stimuli may therefore trigger different control mechanisms. The cued-incentive trials used trigger proactive control mechanisms (Braver, 2012; Krebs & Woldorff, 2017), while incentives presented concurrently with target stimuli trigger immediate control mechanisms, which are highly sensitive to approach/avoidance tendencies (Bargh et al., 1996; Chen & Bargh, 1999; Kozlik et al., 2015). The ERD modulations found in response to positive/negative incentives likely reflect changes in proactive control, which are sensitive to attentional biases made with losses and gains, whereas the reactive control associated directly with incentive presentation is likely to be more reactive to approach/avoidance associations.

Finally, while a sustained increase in power in the theta frequency range was found over frontal midline areas of the scalp throughout the Go/NoGo task, theta-band power did not significantly change across reward or task conditions. Frontal-midline theta-band power enhancements have repeatedly been associated with broad working memory and cognitive control processes, (Gevins et al., 1997; Jensen & Tesche, 2002; Klimesch et al., 2005; Onton et al., 2005). Synchronisation in the theta band is hypothesised to reflect sustained effortful engagement in the face of growing mental fatigue (Umemoto et al., 2019), suggesting that the incentive and task cues used presently caused phasic rather than sustained modulations in effortful engagement and task-relevant cortical activation.

During the discounting task, participants were more willing to engage in higher effort options when incentivised with losses compared to gains. However, individual SVs of effort did not significantly correlate with either the speeding of RTs or increases in anticipatory ERD under gain and loss conditions; similar findings were also shown in our previous experiments (Byrne et al., 2020; Byrne et al., submitted). The

discounting task results show the increased SV often associated with monetary losses (Baumeister, Bratslavsky, Finkenauer, & Vohs, 2001; Krebs & Woldorff, 2017; Rozin & Royzman, 2001; Wright & Rakow, 2017). These results also suggest that the valuation of losses and gains regarding participants' willingness to engage in effortful behaviour does not directly inform the implementation of effortful resources during ongoing effortful engagement, or that the willingness to engage in effortful task employs different valuation processes to those employed by incentive during ongoing effortful engagement.

A probable cause of these divergent results is that the discounting task required participants to choose between two discrete options, while the Go/NoGo task required participants to make the continuous decision to deploy effortful resources over a period of seconds. The discounting and Go/NoGo tasks may therefore recruit different decision-making processes or may be affected by different confounding variables. For example, the decisions made during the discounting task may be confounded by the salience of the incentives offered (Yechiam & Hochman, 2013), while ongoing effortful engagement may be confounded by attentional or approach/avoidance associations made with gains and losses (Buzzell, Beatty, Paquette, Roberts, & McDonald, 2017; Hoofs, Carsten, Boehler, & Krebs, 2019; Houtman & Notebaert, 2013; Pratto & John, 1991; Yechiam & Hochman, 2013).

Previous studies have shown that perceived effort is significantly associated with the electrophysiological movement-related cortical potential (MRCP) preceding effortful movement (Slobounov et al., 2004; de Morree et al., 2012; Lampropoulou & Nowicky, 2012). The MRCP has been localised to sensorimotor areas (Deecke & Kornhuber, 2003; Ikeda & Shibasaki, 2003; Hiroshi Shibasaki & Mark Hallett, 2006; Toma et al., 2002), and is considered to be a direct indicator of central motor command

in active muscle groups (Bötzel et al., 1997). Taken with previous findings, the present results suggest that while participants are able to accurately monitor effortful engagement, the SV of effort does not directly inform effortful engagement, meaning the lack of associations found may not result from an inability of the participants to accurately monitor effortful engagement.

In conclusion, gains/losses and approach/avoidance motor sets act independently during the preparation of a Go/NoGo motor response. Further, neural activation reflecting anticipatory attention is stronger when participants are incentivised with a gain compared to a loss, while activation reflecting motor-approach behaviours increases symmetrically when participants are incentivised with losses and gains. Gains, therefore, likely motivate increased effortful performance relative to losses during proactive control by modulating increased attentional engagement during proactive control rather than motor preparation, and this effect acts independent of approach/avoidance motor tendencies. Finally, the value of effort is not significantly associated with behavioural or cortical oscillatory changes during effortful behaviour. Thus, willingness to engage in effortful tasks may not directly contribute to ongoing effortful engagement under reward or instantaneous states of motor readiness preceding movement.

Chapter 7 –Discussion

7.1 General Discussion

Research investigating the neuroeconomic basis of cognitive effort-based decision-making has previously been aimed towards investigating the effect of effortful requirements on the SV of associated rewards as well as the effect of differing incentives on effortful performance. While the neural underpinnings of reward valuation and cognitive control are relatively well understood, the way differing incentives interact with control systems during effortful engagement has been less well investigated. The implementation of ERD analyses in the experiments discussed in the previous chapters was used to investigate how gains and losses affected activation and inhibition as well as task-relevant cortical processes such as motor preparation and anticipatory attention.

7.2 Summary of Findings

- In all experiments, increasing incentives were found to significantly quicken RTs, and effort-discounting increased in the COGED task with higher effort requirement levels.
- In chapter 4, reward modulated anticipatory cortical oscillatory responses in markedly different ways depending on how the baseline of cortical amplitudes was calculated.
- In experiment 1 of chapter 4, a prominent ERS over frontal and sensorimotor areas was found, reflecting motor inhibition, and reward level sharpened the motor inhibition associated with fast responses.

- In experiment 2 of chapter 4, high rewards resulted in stronger ERD over frontal and posterior-parietal areas of the scalp and over ipsilateral sensorimotor areas in the beta band.
- While losses were more motivating than gains, symmetrical patterns of response-speed and cortical activation were found between gain and loss domains in chapter 5.
- In chapter 6, anticipated gains incentivised faster RTs as well as stronger anticipatory alpha-band ERD over fronto- and posterior-parietal regions of the scalp compared to both loss and no incentive conditions, as did approach motor-sets. However, the effect of incentive and motor-sets did not interact.
- In all reported experiments, no significant association was found between individual effort discounting rates and changes in effortful performance or cortical oscillatory power.

7.3 Themes

Several themes are observed across the experimental portions of the present thesis. The use of ERD measures allowed us to investigate the underlying cortical processes behind effortful implementation in response to different incentive types. Complimentary to ERD measures, the COGED task was used to calculate individual effort-discounting rates in the gain and loss domains. Incentives of differing magnitudes (low/high) and valence (gain/loss) were shown to have differential effects on preparatory ERD in the alpha and beta bands. In the two experiments reported in chapter 4, incentive was shown to modulate either cortical activation or inhibition depending on the structure of the task and the type of baseline used. Alpha ERD over frontal and posterior-parietal regions of the scalp, reflecting anticipatory attention, was found to be sensitive both to incentive magnitude and valence, while beta-band ERD

over bilateral sensorimotor areas was only sensitive to incentive magnitude. Both alpha- and beta-band ERD were modulated by approach/avoidance motor-sets, but the effect of motor-sets and incentives on ERD changes did not interact. Effort-discounting rates increased with higher effort requirement levels, and losses were shown to be more motivating than gains. However, individual effort-discounting rates calculated from the COGED task were not associated with behavioural or ERD changes, indicating that these changes are not directly modulated by economic value.

7.3.1 Changes in cortical processes with reward.

The methodology used throughout the studies reported in the present thesis implemented ERD measures during the anticipatory period of an effortful task in combination with behavioural measures under differing incentive magnitudes or valences. A COGED task (Massar, Lim, Sasmita, & Chee, 2016; Westbrook & Braver, 2015) was employed following the completion of the vigilance or Go/NoGo tasks, and this was used to estimate individual SVs of effort, which were correlated with effortful performance and ERD changes during the effortful task.

Similar to previous research investigating effortful engagement using CV measures (Newlin & Levenson, 1979; Obrist, 2012; Segers, Steendijk, Stergiopulos, & Westerhof, 2001; Wright, 1996; Richter 2008; Wright 1990), the inclusion of preparatory ERD measures allowed us to identify the cortical underpinnings behind the effects of different incentive types on effortful performance. Specifically, ERD measures during the preparatory period of an effortful task allowed us to separate the cortical processes associated with attention, motor preparation, and motor inhibition. Incentives of different magnitudes were compared, as well as positive and negative incentives of equal and differing nominal values. The interaction between incentive valence and approach/avoidance motor sets was also investigated.

If the sustained vigilance task described in chapter 4 was conducted in a block design, with the baseline being taken at the start of the block and reward level consistent across the block, a sustained increase in cortical power in the alpha and beta bands was observed, reflecting an increase in cortical inhibition (Foxe & Snyder, 2011; Fu et al., 2001; Jokisch & Jensen, 2007; Kelly, Lalor, Reilly, & Foxe, 2006; Rihs, Michel, & Thut, 2007; Worden, Foxe, Wang, & Simpson, 2000; Yamagishi et al., 2003). Reward level was shown to interact with the increased inhibition required when preceding faster responses; a significantly stronger inhibitive response preceding fast compared to slow responses was seen only during high-reward trials.

In contrast, if the incentive level changed trial-by-trial and the baseline was taken seconds before the occurrence of the target stimulus, a decrease in cortical power in the alpha and beta bands was observed. ERD in the beta band was found over bilateral sensorimotor areas, likely representing motor preparation (Erbil & Ungan, 2007; Pfurtscheller, Stancak, et al., 1996; Stancak & Pfurtscheller, 1996), and posterior-parietal and frontal ERD in the alpha band was found, likely representing anticipatory attention (Capotosto et al., 2009; Corbetta & Shulman, 2002; Coull, Walsh, Frith, & Nobre, 2003; Kastner & Ungerleider, 2000; Serences & Yantis, 2006). Alpha- and beta-band ERD was shown to be sensitive not only to response-speeds, but also to reward, as it was stronger during high-reward trials.

Taken together, the two experiments presented in chapter 4 show the inhibitive and activation components posited by the horse race model of motor actions (Band & Logan, 2003; Logan & Cowan, 1984; Schultz, 2015), using novel ERD measures. The results showed that cognitive effort is engaged through the strategic activation and inhibition of task-relevant cortical areas only when the offered incentives are sufficiently high. Falling in line with findings showing that trial-by-trial incentive

manipulation promote transient effects (Krebs, Boehler, & Woldorff, 2010; Novak & Foti, 2015; Zhang, Li, Wang, Liu, & Zheng, 2017), while block incentive manipulations emphasise sustained changes (Locke & Braver, 2008; Umemoto & Holroyd, 2015), these results suggest that the holding and release of inhibition is sensitive to sustained changes, while preparatory motor activation is sensitive to transient incentive effects.

The experiment reported in chapter 5 expanded on these findings with the inclusion of graded losses and gains used as incentives during the sustained vigilance and COGED tasks. Symmetrical increases in sensorimotor alpha- and beta-band ERD were found in response to graded gains and losses. The results presented in chapter 5 show that graded losses and gains caused symmetrical increases in cortical activation over the same recording sites, reflecting symmetrical increases in motor preparation (Erbil & Ungan, 2007; Pfurtscheller, Stancak, et al., 1996; Stancak & Pfurtscheller, 1996). The results show a 'U-shaped' relationship between incentive and engagement (Bechara, Damasio, Tranel, & Damasio, 1997; Costantini & Hoving, 1973; Davidson, Ekman, Saron, Senulis, & Friesen, 1990; Ganzach & Karsahi, 1995; Hochman & Yechiam, 2011; Lang, Bradley, & Cuthbert, 1990, 1997; Sokol-Hessner, Camerer, & Phelps, 2013) and show that losses and gains act to modulate reward through similar cortical processes. However, the results presented in chapter 5 did not identify where the divergence occurs between losses and gains regarding their effects on effortful performance.

To directly investigate the interactions between approach/avoidance associations made with positive or negative incentives (Buzzell, Beatty, Paquette, Roberts, & McDonald, 2017; Hoofs, Carsten, Boehler, & Krebs, 2019; Houtman & Notebaert, 2013; Pratto & John, 1991)**,** the experiment reported in chapter 6 measured

ERD changes during the anticipatory period of a Go/NoGo task while participants expected either an approach or avoidance motor response in loss, gain, and no incentive conditions. It was shown that inhibitory motor-sets resulted in significantly smaller ERD in the beta band over bilateral sensorimotor areas and in the alpha band over frontal and posterior-parietal areas. Similarly, losses were associated with weaker ERD in the alpha band over overlapping areas of the scalp overlaying frontal and posterior-parietal cortical regions compared to gains of equal nominal value. However, no interaction was found between the effect of incentives and the effect of approach/avoidance motor-sets on cortical oscillatory changes, indicating that incentive acted independent to approach/avoidance associations. Further, while beta-band ERD over bilateral sensorimotor areas was stronger when participants were offered an incentive compared to no incentive, no significant difference was found between gain and loss conditions.

The ERD measures taken during the experiment described in chapter 6 were able to separate the effects of incentives and approach/avoidance motor sets on patterns of activation reflecting motor preparation and anticipatory attention. The results presented were able to expand on previous behavioural studies investigating the effect of gains and losses on effortful performance by showing how gains and losses modulated proactive control and anticipatory attention (Carsten, Hoofs, Boehler, & Krebs, 2018; Fontanesi, Palminteri, & Lebreton, 2019; Paschke et al., 2015; Potts, 2011).

7.3.2 The effect of gains and losses on cognitive effort

A common theme in the research presented in chapters 5 and 6 is the investigation of the differential effects of gains and losses on discounting rates and effortful performance. In the COGED task, losses were shown to have a significantly

larger AuC than gains, indicating losses were more motivating than gains. However, in both the sustained vigilance and Go/NoGo tasks losses were not found to cause significantly faster RTs than gains when used as incentives.

The behavioural results described in the present thesis match those found in previous experiments. Losses are often found to be more motivating than gains (Baumeister, Bratslavsky, Finkenauer, & Vohs, 2001; Krebs & Woldorff, 2017; Rozin & Royzman, 2001; Wright & Rakow, 2017), but also cause no difference in (Boksem & Tops, 2008; Seifert, Naumann, Hewig, Hagemann, & Bartussek, 2006) or even a deterioration of effortful performance (Carsten, Hoofs, Boehler, & Krebs, 2018; Fontanesi, Palminteri, & Lebreton, 2019; Paschke et al., 2015; Potts, 2011) relative to gains of equal nominal value.

Several hypotheses have been proposed to explain the divergent effect of losses and gains on effortful performance. First, it has been suggested that losses result in a deterioration in effortful performance relative to gains due to approach/avoidance associations made with losses and gains (Chapman, Gallivan, Wong, Wispinski, & Enns, 2015; Zheng et al., 2017). Avoidance associations may cause a deterioration in performance as they cause participants to withdraw from the task, resulting in slower RTs. In contrast, approach associations may cause a relative increase in performance as they cause participants to engage more with the task, resulting in faster RTs (Chen, Lakshminarayanan, & Santos, 2006; De Houwer, Crombez, Baeyens, & Hermans, 2001; Duckworth, Bargh, Garcia, & Chaiken, 2002; Markman & Brendl, 2005; Rinck & Becker, 2007; Solarz, 1960).

Alternately, the divergent effect of losses and gains on effortful performance has been proposed to be the result of attentional saliency, causing losses to distract participants from the primary task goals (Yechiam, Retzer, Telpaz, & Hochman,

2015). The attentional account of the divergent effect of losses and gains on effortful performance falls in line with the attentional model of loss aversion, which suggests that rather than being more motivating than gains, losses simply attract more attentional resources, leading to the illusion of loss-aversion in choice tasks (Yechiam, Retzer, Telpaz, & Hochman, 2015).

The experiment reported in chapter 5 investigated the anticipatory cortical responses associated with graded losses and gains during a cued vigilance task. We showed that graded loses and gains were associated with symmetrical increases in cortical activity over frontal and sensorimotor areas, forming a 'U-shaped' curve with no significant difference between the gradient of the slopes in gain and loss trials. To expand on the approach/avoidance associations made with losses and gains during effortful performance, the experiment presented in chapter 6 investigated the interactive effects of positive and negative incentives on the anticipatory ERD associated with approach/avoidance motor sets during a cued Go/NoGo task. We found weaker alpha-band ERD over frontal and posterior-parietal regions in conditions with avoidance motor sets and when participants were incentivised with losses compared to gains. Similarly, beta-band ERD over bilateral sensorimotor areas was stronger when participants were incentivised with a loss or a gain compared to no incentive conditions, but no difference was found between gain and loss conditions. Further, the hypothesised interaction between approach/avoidance motor sets and positive/negative incentives was not found, indicating that gains and losses acted independently to approach/avoidance tendencies.

The results presented in chapter 5 show that cortical activation associated with motor preparation and anticipatory attention increased symmetrically with graded losses and gains, showing that both incentive types employed similar cortical

processes. This falls in line with classical findings showing a ‘U-shaped’ relationship between the effect of increasing losses and gains on arousal (Bechara, Damasio, Tranel, & Damasio, 1997; Costantini & Hoving, 1973; Davidson, Ekman, Saron, Senulis, & Friesen, 1990; Ganzach & Karsahi, 1995; Hochman & Yechiam, 2011; Lang, Bradley, & Cuthbert, 1990, 1997; Sokol-Hessner, Camerer, & Phelps, 2013). The results therefore expanded on the ‘U-shaped’ relationship between losses and gains with the novel measure of anticipatory ERD, highlighting the cortical processes associated with the increase in effortful performance during a sustained vigilance task. Further, participants were shown to be sensitive to the magnitude of gains, with ERD being stronger in high- compared to low-reward trials, but insensitive to loss magnitude, with no difference found between high- compared to low-reward trials. These results may reflect a process of attentional orienting to the presence of a loss with little processing of the magnitude of the loss itself, while more deliberation is given to the value of the gain to calculate whether it is worth pursuing. This system may have evolved to provide individuals with the means to respond as quickly as possible to threatening stimuli, as any delay or uncertainty could result in significant harm, while being able to spend more time considering whether it is worth pursuing an appetitive outcome without being under any significant threat. However, this interpretation was not directly investigated in the present thesis and requires further investigation to warrant strong consideration.

Expanding on the findings of chapter 5, the results shown in chapter 6 suggest that anticipatory attention was stronger when participants were incentivised with a gain compared to a loss, but that motor-approach behaviours increased symmetrically under losses and gains. The ERD patterns shown therefore support attentional accounts of the divergent effect of losses and gains on effortful performance (Yechiam &

Hochman, 2013; Yechiam, Retzer, Telpaz, & Hochman, 2015), while contradicting approach/avoidance accounts (Buzzell, Beatty, Paquette, Roberts, & McDonald, 2017; Hoofs, Carsten, Boehler, & Krebs, 2019; Houtman & Notebaert, 2013; Pratto & John, 1991).

Participants may have shown increased attention-related ERD in gain trials due to the saliency of losses distracting participants and therefore reducing sustained attention to the task. Alternately, losses may have resulted in an immediate attentional orienting response which faded while they anticipated the Go/NoGo cue, meaning they did not sufficiently prepare for the target stimulus. However, since immediate responses to gain/loss cues were not investigated, a definitive interpretation cannot be made.

However, contrary to the hypotheses made, no significant interaction was found between the effect of approach/avoidance motor-sets and incentive effects on preparatory ERD responses. Previous studies investigating interactive effects between positive/negative incentives and approach/avoidance behavioural tendencies during Go/NoGo tasks have found mixed results. Early studies investigating this interaction showed that gains and losses enhance Go/NoGo performance compatible to the approach/avoidance associations made with the incentives (i.e., gains improve Go RTs and losses improve NoGo stopping rates) (Guitart-Masip et al., 2011; Guitart-Masip et al., 2012; Richter et al., 2014; Hoofs, Böhler, & Krebs, 2019). However, more recent research failed to show significant interactions between incentive valence and Go/NoGo responses (Boehler, Hopf, Stoppel, & Krebs, 2012; Verbruggen & McLaren, 2018; Schevernels, Bombeke, Krebs, & Boehler, 2016). There are several methodological factors which may explain these mixed results, however a key difference in understanding why no interaction was found presently is the placement

of the incentive cue relative to the Go/NoGo stimulus. A stronger interaction between positive/negative incentives is often found when Go/NoGo cues are presented concurrent with incentive information, compared to seconds after the presentation of incentive information (Hoofs, Böhler, & Krebs, 2019). The placement of incentive information relative to the target stimulus may therefore trigger substantially different control mechanisms, which may be differentially affected by incentive valence. The pre-cued trials used in all experiments reported in the present thesis trigger proactive control responses (Braver, 2012; Krebs & Woldorff, 2017), while incentives presented concurrent to Go/NoGo cues trigger immediate control mechanisms (Bargh et al., 1996; Chen & Bargh, 1999; Kozlik et al., 2015). Proactive control mechanisms investigated may not be sensitive to approach/avoidance responses made immediately after the presentation of incentive information, and the differences found may be reflective of tonic changes in attention or effortful engagement under different incentive conditions.

The experiment discussed in chapter 6 investigated passive rather than active avoidance, as the participants were required to make no response to NoGo stimuli, rather than actively avoiding an aversive stimulus (Binti Affandi et al., 2021; Riley & Foss, 1991). The present results may therefore not be applicable to situations where participants are required to actively approach or avoid an aversive stimulus. This is particularly relevant as active inhibition is associated with much stronger signs of arousal compared to passive inhibition (Binti Affandi et al., 2021; Riley & Foss, 1991), meaning it may have marked effects on effortful performance when associated with a loss or a gain.

7.3.3 Fronto- and posterior-parietal activation

A common theme reported across the experiments discussed in the present thesis was the observation of patterns of alpha-band ERD over frontal and posterior parietal areas of the scalp. Frontal and posterior-parietal alpha-band ERD was shown to be sensitive to incentive magnitude in chapter 4, as well as incentive modality in chapter 6.

Alpha-band ERD over fronto-central and posterior parietal regions is most commonly associated with activation in the FPN, where frontal regions control anticipatory attention in occipital and parietal occipital cortical regions through the suppression of ongoing alpha rhythms (Corbetta, Patel, & Shulman, 2008; Coull et al., 2003; Kastner & Ungerleider, 2000; Serences & Yantis, 2006). This interpretation is supported by TMS studies reporting deficits in visual processing and posterior-parietal ERD following TMS interference of posterior parietal and fronto-parietal regions (Capotosto et al., 2009)). The patterns of alpha band ERD reported in chapters 4 and 6 can therefore be viewed as reflecting the anticipatory attention required to detect the target stimulus to respond as quickly and accurately as possible to the occurrence of Go/NoGo cues. The results presented in chapter 4 support this interpretation of frontal and posterior-parietal alpha-band ERD, as fast responses were preceded by a significantly stronger ERD compared to slow responses.

Expanding on these findings, the results reported in chapter 6 show that anticipatory attention was sensitive both to incentive valence and to approach/avoidance motor sets induced by task demands. Alpha-band ERD over frontal and posterior-parietal scalp regions was weaker when avoidance motor sets were induced, and when participants were incentivised with a loss over a gain. The results presented in chapter 6, therefore, provide a novel explanation for the divergent

effect of losses and gains on effortful performance, suggesting that losses impair performance relative to gains as they result in reduced attention to primary task demands. Losses were suggested to impair performance due to their increased attentional saliency, causing participants to pay attention to the loss itself and thereby distracting them from the task requirements.

7.3.4 Bilateral sensorimotor beta-band ERD

While anticipatory attention is an important task-relevant cognitive process for fast responses to Go cues, pre-prepared motor activation is also required to execute a speeded motor response once the Go cue is recognised (Band & Logan, 2003; Logan & Cowan, 1984; Schultz, 2015). The required pre-prepared motor response was reflected in the ERD measures taken in the present thesis as a beta-band ERD overlaying sensorimotor regions of the scalp and was found in all reported experiments. Sensorimotor beta-band ERD was shown to be sensitive to reward magnitude, response-speed, and approach/avoidance motor sets, but not to reward modality

In the experiment reported in chapter 4, sensorimotor beta-band ERD was significantly stronger when preceding a fast compared to a slow response and during high-reward compared to low- and no-reward trials. Similarly, this ERD was stronger in high-incentive compared to low-incentive and no-incentive trials in chapter 5, and was stronger when participants were offered an incentive compared to no incentive in chapter 6. However, no significant difference was found between the slope of the ERD under graded losses and gains in the results reported in chapter 5, forming a U-shaped curve, where the strength of the ERD increased as both positive and negative incentives increased in magnitude. Similarly, no significant difference was found between gain and loss conditions in chapter 6.

Sensorimotor ERD in the beta band likely reflects increased motor preparation during the anticipation of the target stimulus (Erbil & Ungan, 2007; Pfurtscheller, Stancak, et al., 1996; Stancak & Pfurtscheller, 1996), originating from the peri-Rolandic regions (Murthy & Fetz, 1996; Pfurtscheller & Berghold, 1989; Pfurtscheller & Neuper, 1997; Schnitzler, Salenius, Salmelin, Jousmaki, & Hari, 1997). This view is supported by the results presented in this thesis, as sensorimotor ERD in the beta band was generally significantly correlated with RTs and was stronger preceding fast compared to slow movements.

Previous research investigating ERD changes during Go/NoGo responses has found no significant differences in the alpha-band (Filipović, Jahanshahi, & Rothwell, 2001; Alegre et al., 2004), but a stronger beta-band ERD during movement initiation compared to inhibition (Alegre et al., 2004). Further, investigating ERD changes during proactive control, Liebrand, Pein, Tzvi, and Krämer (2017) showed significantly weaker alpha-band ERD over posterior-parietal regions and stronger sensorimotor beta-band ERD when participants prepared a Go response, compared to trials when they were uncertain as to whether they would be required to execute a subsequent Go or NoGo response. While these findings seem to contradict the results found in chapter 6, this divergence may be due to the respective cue probabilities used. In the experiment reported presently, participants expected a Go/NoGo cue with a fixed probability of .75 in each condition, while in the experiment reported by Liebrand, Pein, Tzvi, and Krämer (2017) trials with a 100% probability of a Go response were compared to trials with equiprobable chances of the occurrence of a subsequent Go/NoGo cue. It therefore seems that anticipatory alpha-band ERD is sensitive to attention or overall task engagement, while beta-band ERD reflects the preparation or maintenance of approach motor responses.

Interestingly, in the results shown in chapters 4 and 6, high incentives were found not only to increase the strength of sensorimotor ERD, but also to affect its laterality. In chapter 4, a contralateral sensorimotor beta-band ERD was found in low- and no-incentive conditions, an effect which became bilateral under the high-reward condition. Similarly, in the results presented in chapter 6, a significant main effect of reward on beta-band ERD was found in a cluster of electrodes overlaying ipsilateral areas of the sensorimotor cortex while that overlaying contralateral areas remained constant across reward levels.

While bilateral sensorimotor ERD is most closely associated with movement execution (Alegre et al., 2006; Cassim et al., 2000; Crone et al., 1998; Doyle, Yarrow, & Brown, 2005; Erbil & Ungan, 2007; Kilavik et al., 2012; Omlor, Patino, Mendez-Balbuena, Schulte-Monting, & Kristeva, 2011; Pfurtscheller, Stancak, & Edlinger, 1997; Stancak & Pfurtscheller, 1996; Tzagarakis, Ince, Leuthold, & Pellizzer, 2010; Wheaton, Fridman, Bohlhalter, Vorbach, & Hallett, 2009), it has also been shown to precede movements with a higher rate of force (Hortobagyi, Taylor, Petersen, Russell, & Gandevia, 2003; Perez & Cohen, 2008; Stedman, Davey, & Ellaway, 1998; Stinear, Walker, & Byblow, 2001; Tinazzi & Zanette, 1998). Ipsilateral beta-band ERD has been proposed to represent interhemispheric inhibition (Fujiyama, Hinder, & Summers, 2013; Welniarz, Dusart, Gallea, & Roze, 2015), preventing mirror movements under cases of high motor preparation. Bilateral sensorimotor ERD has also been associated with deteriorating motor processes with age (Derambure et al., 1993), where a stronger ipsilateral pre-movement ERD (Vallesi, McIntosh, Kovacevic, Chan, & Stuss, 2010) and a weaker contralateral ERD (Naccarato et al., 2006; Ward & Frackowiak, 2003; Ward et al., 2008) is commonly found in older participants.

The associations drawn in the present research between laterality and reward give further insight into the functional role of asymmetry in the motor cortex. This suggests that the bilateral ERD previously shown preceding high-force movements and in older participants reflects higher physical effort causing an overflow of activation from the contralateral motor cortex into the ipsilateral cortex (Fujiyama, Hinder, & Summers, 2013; Welniarz, Dusart, Gallea, & Roze, 2015).

7.3.5 Lack of significant theta-band effects.

A theta-band ERS was hypothesised to be found over fronto-central areas of the scalp, and to increase with reward and when preceding fast compared to slow responses. However, while the expected pattern of frontal-midline theta-band ERS was found, this was not significantly modulated by incentives, response-speeds, or task-conditions.

An increase in cortical power in the theta band over fronto-central areas of the scalp is commonly found during the active maintenance of high-level cognitive processes such as working memory, novelty detection, and cognitive control (Cavanagh, Zambrano-Vazquez, & Allen, 2012; Itthipuripat, Wessel, & Aron, 2013; Jacobs, Hwang, Curran, & Kahana, 2006; Rutishauser, Ross, Mamelak, & Schuman, 2010), and during effortful listening tasks (Rönnberg et al., 2013; Rönnberg, Rudner, Foo, & Lunner, 2008). For this reason, fronto-central theta-band ERS is often considered to directly reflect the sustained deployment of cognitive effort (Itthipuripat et al., 2013).

However, theta-band ERS may be reflective of tonic rather than phasic cognitive effort. Fronto-central theta-band ERS is generally only found during periods of extended effortful engagement (Asada, Fukuda, Tsunoda, Yamaguchi, & Tonoike, 1999; Barwick, Arnett, & Slobounov, 2012; Hsieh & Ranganath, 2014; Ishii et al.,

1999; Mitchell, McNaughton, Flanagan, & Kirk, 2008; Paus et al., 1997; Wascher et al., 2014). It has been suggested that theta-band activation reflects the sustainment effortful behaviour in the face of growing mental fatigue rather than phasic increases in cognitive effort in response to incentive or task cues (Umemoto, Inzlicht, & Holroyd, 2019).

The present lack of significant findings in the theta band suggest that incentives only caused phasic, short-term modulations in effortful engagement on a trial-by-trial basis rather that sustained changes in effortful engagement. This may be due to the current task structure used, as incentive cues were presented two seconds prior to the occurrence of the target stimulus, meaning a sustained modulation of effortful engagement was not required. The present results may therefore lack generalisability to tasks which require sustained effortful engagement, as is common in more ecologically valid effortful situations.

7.3.6 Associations with effort discounting rates

All experiments discussed in the present thesis used a COGED task to calculate individual effort-discounting rates the across multiple effort levels, and the experiments reported in chapters 5 and 6 compared the SV of effort across gain and loss modalities.

The SV of effort calculated during the COGED task in the present thesis matches the results found by previous experiments. We first found in all experiments, and as hypothesised, that rewards were discounted more sharply if participants were required to complete the vigilance task again for thirty minutes compared to five minutes. Second, in chapters 5 and 6, where loss and gain conditions were included in the task, participants were more willing to engage in the high effort option when avoiding losses compared to incentive with gains, matching the classical finding of

loss-aversion in the domain of cognitive effort (Baumeister, Bratslavsky, Finkenauer, & Vohs, 2001; Krebs & Woldorff, 2017; Rozin & Royzman, 2001; Wright & Rakow, 2017). However, contrary to the findings of previous research (Massar 2016), a common theme across all chapters is that individual effort-discounting rates did not significantly correlate with changes in effortful performance or ERD during differing incentive trials.

It is likely that individual discounting rates that are implemented during the decision to engage in an effortful task are not directly modulated during the effortful engagement required for an ongoing task. A probable cause of the lack of associations between SV and effortful engagement found presently is that the discounting task required participants to choose between a pair of discrete options, while the Go/NoGo and vigilance tasks required participants to continuously deploy and maintain effortful resources. The effortful decisions made during the discounting and sustained vigilance tasks also exist along different phases of the Rubicon model of action (Gollwitzer, 1990), with the discounting task recruiting behaviour primarily existing in the pre-decisional phase, and the sustained vigilance and Go/NoGo tasks recruiting behaviour occurring primarily in the volitional stage. Further, significantly different mindsets have been shown to become dominant during each phase of the decision (Gollwitzer, 1990; Gollwitzer, 1999; Heckhausen & Gollwitzer, 1987) (e.g., a deliberative mindset during the pre-decisional phase, moving to a actional mindset in the volitional phase). The mindsets required during the COGED task are likely significantly different to those made in the sustained-vigilance and Go/NoGo tasks, meaning it may not be possible to directly compare behaviour observed during these tasks.

The discounting task may therefore recruit different decision-making processes to those employed during the Go/NoGo and sustained vigilance tasks. Specifically, the

cognitive frames of decision-outcomes and perceived fairness have been shown to directly affect participants' effortful engagement with an associated task (Brooks, Stremitzer, & Tontrup, 2017; Church, Libby, & Zhang, 2008; Gose & Sadrieh, 2012; Hannan, Hoffman, & Moser, 2005; Van de Weghe & Bruggeman, 2006). It has also been suggested that the observation of loss-aversion depends more on the salience of losses over gains rather than being due to losses being subjectively more motivating than gains.

Of particular note in the research in the present thesis is cognitive fatigue and the aversion to cognitively demanding tasks associated with it (Arai, 1912; Blain, Hollard, & Pessiglione, 2016; Hagger, Wood, Stiff, & Chatzisarantis, 2010; Scerbo, 2001). In the experiments discussed, participants were required to complete the COGED task after they had spent an extended period of time engaging with either the sustained vigilance or Go/NoGo task and would therefore likely be significantly fatigued when completing the COGED task. The discounting rates calculated in the experiments discussed were likely much higher than would be found in a sample of well-rested participants, meaning that the discounting results may lack generalisability. Further, participants may have made decisions primarily based on individual fatigue, rather than SVs of effort, providing a potential explanation for the lack of association between discounting rates and ERD/effortful performance. It is recommended that future research using these methods takes the effect of cognitive fatigue into account when considering their experimental design by, for example, counterbalancing the order of the sustained vigilance and COGED tasks.

7.3.7 Implications to theories of cognitive effort

Cognitive effort and prolonged cognitive control are commonly seen as costly (Hasher, 1979; Kaplan & Berman, 2010; Schneider & Shiffrin, 1977), and effortful

resources are thought to be deployed proportional to the SV of associated incentives (Walton, Kennerley, Bannerman, Phillips, & Rushworth, 2006). Several theories have been proposed to explain the aversive and fatiguing nature of cognitive effort (Christie & Schrater, 2015; Gailliot & Baumeister, 2007; Kurzban, 2016), however each has its own limitations, and no single theory comprehensively explains the aversive nature of cognitive effort.. Two schools of thought have emerged, explaining the costs of cognitive effort; resource-limited and cost benefit models (Westbrook & Braver, 2015). Resource-limited models posit that the aversive nature of effortful tasks comes from the depletion of a specific metabolic resource, namely blood-glucose levels (Gailliot & Baumeister, 2007). In contrast, cost benefit models of cognitive effort describe effortful tasks as being aversive when the opportunity costs associated with engaging effortful resources outweighs the SV of associated outcomes (Lazarus, 1993; Tooby & Cosmides, 2008). Opportunity costs that may be associated with cognitive effort include patterns of reciprocal inhibition associated with attentional engagement given in a specific domain (e.g., during visual attention tasks an individual must inhibit auditory processing) (REF).

The results presented in chapter 4 appear to support opportunity cost over resource-limited models of cognitive effort, as they show that reward modulated strategic cortical activation and inhibition, rather than causing global increases in metabolic activity. In experiment 1 of chapter 4, a sustained increase in oscillatory power reflecting cortical inhibition interacted with reward and response-speeds. In experiment 2, a phasic decrease in cortical power, reflecting cortical activation, was shown to be modulated by reward level. The results presented across both experiments of chapter 4 show that cognitive effort was not associated with global increases in neural activity posited by resource-limited models, but instead was associated with

strategic modulations in cortical inhibition and activation, which may explain the opportunity costs associated with cognitive effort.

However, the results presented in chapters 5 and 6 suggest that the cost-benefit analysis associated with cognitive effort in opportunity cost models are not made based on the SV of reward alone. First, the results presented in chapter 5 showed that while losses were more motivating than gains, graded losses and gains were associated with symmetrical increases in response-speeds and cortical activation over task-relevant areas. It, therefore, appears likely that cognitive effort is deployed in response to incentive magnitude, although factors beyond SV may impair or enhance the deployment of effortful resources, or the effectiveness of effortful behaviour.

Expanding on the results presented in chapter 5, the results presented in chapter 6 showed that losses were associated with deteriorations in activation patterns associated with attention, rather than approach/avoidance responses. Thus, the divergent effect of losses and gains may be due to the attentional saliency of the incentives, causing losses to distract participants from primary task goals (Yechiam, Retzer, Telpaz, & Hochman, 2015), meaning that effortful resources may be deployed in response to the attentional salience of an offered reward, rather than directly as a result of the incentive's SV.

Further, it is important to note that opportunity cost models are primarily formulated to explain choice behaviour regarding prospective effort requirements (Kurzban, 2016). The opportunity costs associated with an effortful action may become insignificant once the individual has committed to pursuing a specific goal, an interpretation supported by mindset research investigating the different stages of the Rubicon model of action (Gollwitzer & Bargh, 1996). The consideration of opportunity costs may therefore only be appropriate when considering the COGED

task results, but not ERD/behavioural results found during the sustained vigilance and Go/NoGo tasks. This means that, while the results discussed in chapter 4 appear to support opportunity cost over resource-limited models of effort, these interpretations can only be made tentatively as the ERD measures used presently did not directly investigate the hypotheses made by either account.

The results discussed in the present thesis fall in line with the predictions made by motivational intensity theory (Richter, 2015; Brehm, & Self, 1989; Gendolla, Wright, & Richter, 2012; Richter, 2013; Wright, 2008; Wright & Pantaleo, 2013; Richter, Gendolla, & Wright, 2016), by showing proportional increases in effortful behaviour to incentive magnitude under conditions of unclear and unfixed difficulty. However, the results discussed presently may not be applicable to tasks with clear difficulty, such as the N-back working memory task, where effortful deployment may be more sensitive to task difficulty than incentive magnitude.

In conclusion, the results presented in the present thesis suggest that cognitive-effort is deployed through the strategic allocation of task-relevant cortical activation and inhibition proportional to the opportunity costs of effortful behaviour. However, the deployment of effortful resources may be confounded by factors beyond the SV of the offered incentives, such as attentional biases or framing effects.

7.4 Limitations

In the experiments described presently, a significant limitation is that only small monetary incentives were used (10 p). While on aggregate these incentives became significant (£10), they may not have been large enough to elicit a strong response or incentivise high levels of cognitive effort alone. Further, in the experiments reported in chapters 4 and 5, where graded incentives were used, only two incentive magnitudes were used, as well as the no incentive condition. The incentives

used means that the exact shape and slope of the ERD and RT effects could not be established to a high degree of resolution. Therefore, the ERD patterns found in the present thesis could not be effectively described using exponential, hyperbolic, or additive utility models.

A primary issue in the current set of studies is the predominant use of undergraduate and postgraduate students as participations. Of key consideration is the age of the participants. The mean age in the reported experiments ranged from 23.34 to 24.48. The sample used may not be generalisable to older individuals as the economic valuation of cognitive effort has been found to change with age. Further, motor function and inhibition are key factors which underlie age-related cognitive decline, causing a deterioration in fine motor control and a slowing of movements (Maes, Gooijers, Orban de Xivry, Swinnen, & Boisgontier, 2017; Rosso et al., 2013; Seidler et al., 2010). Sensorimotor movement-related beta-band ERD and absolute beta-band power has also been reported to be significantly stronger in older samples (Bardouille & Bailey, 2019; Heinrichs-Graham et al., 2018; Hübner, Godde, & Voelcker-Rehage, 2018; Rossiter, Davis, et al., 2014; Sailer, Dichgans, & Gerloff, 2000; Heinrichs-Graham et al., 2018; Hübner et al., 2018; Koyama, Hirasawa, Okubo, & Karasawa, 1997; Veldhuizen, Jonkman, & Poortvliet, 1993). As movement-related potentials, particularly sensorimotor beta-band ERD, were a key measure in the present research, generalisability across age-groups may be difficult to establish. A student population may also have a lower income than other populations, and may subsequently respond significantly differently in economic situations than would be found in a sample with a more diverse range of incomes.

Finally, the tasks employed in the present thesis may not be generalisable to more ecologically valid conditions where effortful engagement is required, and the

ERD patterns examined may not be applicable to other effortful tasks often used in laboratory settings. The vigilance task and Go/NoGo task used presently require two primary cognitive and cortical processes; motor control and anticipatory attention. While both motor control and anticipatory attention may be effortful, there are a wide range of other processes which may also be associated with cognitive effort and are investigated using alternate tasks. For example, the N-back memory test requires the maintenance of working memory stores, which were not investigated in the present thesis. The vigilance and Go/NoGo tasks also do not account for the various other factors which may be associated with effortful engagement in more ecologically valid settings, such as long-term goals associated with the engagement and distractors in the environment.

7.5 Suggestions for Future Research

The present thesis contributes to the literature regarding the valuation and engagement of cognitive effort with incentives primarily by the addition of ERD measures, which showed by what mechanism incentives boost effortful engagement and how cortical processes are associated with performance and the subjective valuation of effort.

The use of graded incentives allowed us to investigate how incentive magnitude affected the cortical processes associated with effortful engagement, and further how different incentive type (e.g., gains and losses) affected effortful cortical processes differently. Previous studies have modelled the discounting effect of cognitive effort as forming a hyperbolic curve (Green, Fry, & Myerson, 1994; Green & Myerson, 2004; Green, Myerson, Oliveira, & Chang, 2013; Odum, Baumann, & Rimington, 2006). Further research which used similar methods to those presented in

this thesis but with the inclusion of more incentive levels, and especially larger incentives, could provide an ERD function which could be compared to the hyperbolic function of effort more closely. Using methods such as these, it would also be of use to compare the main effects and interactions with effort and other similar discounting factors such as delay and probability discounting.

Regarding the previously discussed limitation of the samples used for the research described in the present thesis, it would be useful to use the methods developed here to compare the effortful engagement of different populations of participants, such as by comparing age groups, or participants diagnosed with clinical disorders such as depression and schizophrenia against neurotypical controls. For example, by comparing younger and older participants in a between-samples design, a great deal of insight could be gained regarding the causal factor behind the differences in effortful discounting and engagement between these two groups.

Finally, it may be of use to investigate the ERD patterns of activation associated with cognitive effort in more ecologically valid conditions. This could be achieved by adding visual or auditory distractors to the environment during the anticipation period, or by making the task more representative of a video game or another effortful task which the participant may engage in regularly in their day-to-day life. Using more a more realistic task may help us to further understand the neural processes behind effortful engagement in these situations.

7.6 Concluding Remarks

While the effect of incentive magnitude and valence on effortful behaviour and physiological measures associated with effortful engagement has previously been investigated, the electrophysiological correlates of this behaviour remains unclear. The

current thesis described the effect of incentive magnitude and valence on cortical oscillatory activity associated with cortical activation and inhibition during differing task conditions. Matching previous studies, decreasing RTs were found with both the presence and magnitude of positive and negative incentives. However, individual discounting rates were not significantly associated with changes in RTs or ERD under differing rewards in any of the studies reported presently. Additionally, ERD responses were found to reflect behavioural performance, with stronger alpha- and beta-band ERD found over frontal, posterior parietal, and sensorimotor regions under high incentive conditions. However, while losses were found to be more subjectively motivating than gains, they did not improve effortful performance relative to gains of equal nominal value when used as incentives. Further, the divergent effect of losses and gains was revealed to be reflected in a stronger anticipatory ERD in the alpha band over frontal and posterior-parietal regions of the scalp, and this did not interact with approach/avoidance task expectations.

These findings contribute to the literature concerning the effect of incentive and effort-discounting rates on the deployment of effortful resources by identifying the role of specific cortical oscillatory changes during effortful engagement. Although behavioural and physiological measures are useful for measuring effortful engagement and outcomes, they fail to measure the cortical processes underpinning effortful behaviour. The present results suggest that monetary incentives modulate effort through the strategic activation and inhibition of task-related cortical areas, resulting in symmetrical increases in effortful engagement in response to losses and gains of increasing magnitude. However, it seems that the SV of incentives does not directly inform effortful engagement, which may be modulated by factors such as attentional biases and framing effects.

In closing, the current thesis has provided a detailed description of the cortical oscillatory dynamics underpinning effortful engagement under differing reward magnitudes and modalities. The utilisation of preparatory ERD measures allowed for the measurement of cortical processes associated with motor activation, inhibition, and anticipatory attention separately, in contrast to behavioural studies which are unable to make strong inferences in this regard. We hope these methods can be used in the future to shed further light on the differential effects on incentive on effortful engagement.

References

Aarts, H., Custers, R., & Marien, H. (2008). Preparing and motivating behavior outside of awareness. *Science*, 319(5870), 1639. doi:10.1126/science.1150432

Aarts, E., Nusselein, A., Smittenaar, P., Helmich, R. C., Bloem, B. R., & Cools, R. (2014). Greater striatal responses to medication in Parkinson′ s disease are associated with better task-switching but worse reward performance. *Neuropsychol, 62*, 390-397. doi:10.1016/j.neuropsychologia.2014.05.023

Aarts, E., Wallace, D. L., Dang, L. C., Jagust, W. J., Cools, R., & D'Esposito, M. (2014). Dopamine and the cognitive downside of a promised bonus. *Psychol Sci, 25*(4), 1003-1009. doi:10.1177/0956797613517240

Abdellaoui, M., Bleichrodt, H., & Paraschiv, C. (2007). Loss aversion under prospect theory: a parameter-free measurement. *Manag Sci, 53*(10), 1659-1674. doi:10.1287/mnsc.1070.0711

Achim, A. (2001). Statistical detection of between-group differences in event-related potentials. *Clin Neurophysiol, 112*(6), 1023-1034. doi:10.1016/s1388-2457(01)00519-3

Acikalin, M. Y., Gorgolewski, K. J., & Poldrack, R. A. (2017). A coordinate-based meta-analysis of overlaps in regional specialization and functional connectivity across subjective value and default mode Networks. *Front Neurosci, 11*, 1. doi:10.3389/fnins.2017.00001

Ackerman, P. L. (2011). *Cognitive fatigue: multidisciplinary perspectives on current research and future applications*. New York: American Psychological Association.

Adolphs, R., Tranel, D., Damasio, H., & Damasio, A. (1994). Impaired recognition of emotion in facial expressions following bilateral damage to the human amygdala. *Nature*, 372(6507), 669-672. doi:10.1038/372669a0

Ahlfors, S. P., Han, J., Belliveau, J. W., & Hamalainen, M. S. (2010). Sensitivity of MEG and EEG to source orientation. *Brain Topogr, 23*(3), 227-232. doi:10.1007/s10548-010-0154-x

Ahveninen, J., Lin, F. H., Kivisaari, R., Autti, T., Hämäläinen, M., Stufflebeam, S., . . . Kähkönen, S. (2007). MRI-constrained spectral imaging of Benzodiazepine modulation of spontaneous neuromagnetic activity in human cortex. *Neuroimage, 35*(2), 577-582. doi:10.1016/j.neuroimage.2006.12.033

Aine, C. J. (1995). A conceptual overview and critique of functional neuroimaging techniques in humans: I. MRI/FMRI and PET. *Crit Rev Neurobiol, 9*(2-3), 229-309.

Ainslie, G. (1975). Specious reward: A behavioral theory of impulsiveness and impulse control. *Psychol Bull, 82*(4), 463-496. doi:10.1037/h0076860

Akerlof, G. A., & Yellen, J. L. (1990). The fair wage-effort hypothesis and unemployment. *Quart J of Econ, 105*(2), 255-283. doi:10.2307/2937787

Alegre, M., Gurtubay, I. G., Labarga, A., Iriarte, J., Malanda, A., & Artieda, J. (2003). Alpha and beta oscillatory changes during stimulus-induced movement paradigms: effect of stimulus predictability. *Neuroreport, 14*(3), 381-385. doi:10.1097/00001756-200303030-00017

Alegre, M., Gurtubay, I. G., Labarga, A., Iriarte, J., Valencia, M., & Artieda, J. (2004). Frontal and central oscillatory changes related to different aspects of the motor process: a study in go/no-go paradigms. *Exp Brain Res*, 159(1), 14-22. doi:10.1007/s00221-004-1928-8

Alegre, M., Imirizaldu, L., Valencia, M., Iriarte, J., Arcocha, J., & Artieda, J. (2006). Alpha and beta changes in cortical oscillatory activity in a Go/No Go

randomly-delayed-response choice reaction time paradigm. *Clin Neurophysiol, 117*(1), 16-25. doi:10.1016/j.clinph.2005.08.030

Alonso, J. F., Romero, S., Mañanas, M., Rojas, M., Riba, J., & Barbanoj, M. J. (2015). Evaluation of multiple comparison correction procedures in drug assessment studies using LORETA maps. *Med Biol Eng Comput, 53*(10), 1011-1023. doi:10.1007/s11517-015-1315-6

Amemori, K., & Graybiel, A. M. (2012). Localized microstimulation of primate pregenual cingulate cortex induces negative decision-making. *Nat Neurosci,* 15(5), 776-785. doi:10.1038/nn.3088

Amin, H., U., Malik, A., S., Hussain, M., Kamel, N., & Chooi, W. (2014). Brain behavior during reasoning and problem solving task: an EEG study. Paper presented at the 2014 5th International Conference on Intelligent and Advanced Systems (ICIAS).

Andersen, P., & Andersson, S. A. (1968). *Physiological basis of the alpha rhythm* (Vol. 1). New York: Plenum Publishing Corporation.

Anderson, J. S., Carandini, M., & Ferster, D. (2000). Orientation tuning of input conductance, excitation, and inhibition in cat primary visual cortex. *J Neurophysiol, 84*(2), 909-926. doi:10.1152/jn.2000.84.2.909

Anderson, K. L., & Ding, M. (2011). Attentional modulation of the somatosensory mu rhythm. *Neurosci, 180,* 165-180. doi:10.1016/j.neuroscience.2011.02.004

Andreou, P., Neale, B. M., Chen, W., Christiansen, H., Gabriels, I., Heise, A., . . . Kuntsi, J. (2007). Reaction time performance in ADHD: improvement under fast-incentive condition and familial effects. *Psychol Med, 37*(12), 1703-1715. doi:10.1017/s0033291707000815

Andres, P., Guerrini, C., Phillips, L. H., & Perfect, T. J. (2008). Differential effects of aging on executive and automatic inhibition. *Dev Neuropsychol, 33*(2), 101-123. doi:10.1080/87565640701884212

Androulidakis, A. G., Doyle, L. M., Gilbertson, T. P., & Brown, P. (2006). Corrective movements in response to displacements in visual feedback are more effective during periods of 13-35 Hz oscillatory synchrony in the human corticospinal system. *Eur J Neurosci, 24*(11), 3299-3304. doi:10.1111/j.1460-9568.2006.05201.x

Androulidakis, A. G., Doyle, L. M., Yarrow, K., Litvak, V., Gilbertson, T. P., & Brown, P. (2007). Anticipatory changes in beta synchrony in the human corticospinal system and associated improvements in Task-Performance. *Eur J Neurosci, 25*(12), 3758-3765. doi:10.1111/j.1460-9568.2007.05620.x

Angelidis, A., Hagenaars, M., van Son, D., van der Does, W., & Putman, P. (2018). Do not look away! Spontaneous frontal EEG theta/beta ratio as a marker for cognitive control over attention to mild and high threat. *Biol Psychol, 135*, 8-17.

Anguera, J. A., Boccanfuso, J., Rintoul, J. L., Al-Hashimi, O., Faraji, F., Janowich, J., . . . Gazzaley, A. (2013). Video game training enhances cognitive control in older adults. *Nature, 501*(7465), 97-101. doi:10.1038/nature12486

Arai, T. (1912). *Mental fatigue*. Columbia University.

Arkes, H. R., Joyner, C. A., Pezzo, M. V., Nash, J. G., Siegel-Jacobs, K., & Stone, E. (1994). The psychology of windfall gains. *Organizational behavior and human decision processes, 59*(3), 331-347. doi:10.1006/obhd.1994.1063

Arnal, L. H., & Giraud, A. L. (2012). Cortical oscillations and sensory predictions. *Trends Cogn Sci, 16*(7), 390-398. doi:10.1016/j.tics.2012.05.003

Arnau, S., Mockel, T., Rinkenauer, G., & Wascher, E. (2017). The interconnection of mental fatigue and aging: An EEG study. *Int J Psychophysiol, 117*, 17-25. doi:10.1016/j.ijpsycho.2017.04.003

Arnsten, A. F. (1998). Catecholamine modulation of prefrontal cortical cognitive function. *Trends Cogn Sci, 2*(11), 436-447. doi:10.1016/S1364-6613(98)01240-6

Arnsten, A. F., Wang, M. J., & Paspalas, C. D. (2012). Neuromodulation of thought: flexibilities and vulnerabilities in prefrontal cortical network synapses. *Neuron, 76*(1), 223-239. doi:10.1016/j.neuron.2012.08.038

Aron, A. R. (2007). The neural basis of inhibition in cognitive control. *Neurosci, 13*(3), 214-228. doi:10.1177/1073858407299288

Aron, A. R., Dowson, J. H., Sahakian, B. J., & Robbins, T. W. (2003). Methylphenidate improves response inhibition in adults with attention-deficit/hyperactivity disorder. *Biol Psychiatry, 54*(12), 1465-1468. doi:10.1016/S0006-3223(03)00609-7

Aron, A. R., Durston, S., Eagle, D. M., Logan, G. D., Stinear, C. M., & Stuphorn, V. (2007). Converging evidence for a fronto-basal-ganglia network for inhibitory control of action and cognition. *J Neurosci, 27*(44), 11860-11864. doi:10.1523/JNEUROSCI.3644-07.2007

Aron, A. R., & Poldrack, R. A. (2005). The cognitive neuroscience of response inhibition: relevance for genetic research in attention-deficit/hyperactivity disorder. *Biol Psychiatry, 57*(11), 1285-1292. doi:10.1016/j.biopsych.2004.10.026

Aron, A. R., & Poldrack, R. A. (2006). Cortical and subcortical contributions to stop signal response inhibition: role of the subthalamic nucleus. *J Neurosci, 26*(9), 2424-2433. doi:10.1523/jneurosci.4682-05.2006

Aron, A. R., Robbins, T. W., & Poldrack, R. A. (2014). Inhibition and the right inferior frontal cortex: one decade on. *Trends Cogn Sci, 18*(4), 177-185. doi:10.1016/j.tics.2013.12.003

Asada, H., Fukuda, Y., Tsunoda, S., Yamaguchi, M., & Tonoike, M. (1999). Frontal midline theta rhythms reflect alternative activation of prefrontal cortex and anterior cingulate cortex in humans. *Neurosci Lett,* 274(1), 29-32. doi:10.1016/s0304-3940(99)00679-5

Asci, O., Braem, S., Park, H., Boehler, C. N., & Krebs, R. M. (2019). Neural correlates of reward-related response tendencies in an equiprobable Go/NoGo task. *Cognitive, Affective, & Behavioral Neuroscience*, 1-13. doi:10.3758/s13415-019-00692-5

Assmus, A., Marshall, J. C., Noth, J., Zilles, K., & Fink, G. R. (2005). Difficulty of perceptual spatiotemporal integration modulates the neural activity of left inferior parietal cortex. *Neurosci, 132*(4), 923-927. doi:10.1016/j.neuroscience.2005.01.047

Atkinson, J. W., & Raynor, J. O. (1978). *Personality, motivation, and achievement:* Hemisphere.

Aurlien, H., Gjerde, I. O., Aarseth, J. H., Eldøen, G., Karlsen, B., Skeidsvoll, H., & Gilhus, N. E. (2004). EEG Background activity described by a large computerized database. *Clin Neurophysiol, 115*(3), 665-673. doi:10.1016/j.clinph.2003.10.019

Babiloni, C., Babiloni, F., Carducci, F., Cincotti, F., Cocozza, G., Del Percio, C., . . . Rossini, P. M. (2002). Human cortical electroencephalography (EEG) rhythms during the observation of simple aimless movements: a high-resolution eeg study. *Neuroimage, 17*(2), 559-572. doi:10.1006/nimg.2002.1192

Babiloni, C., Brancucci, A., Arendt-Nielsen, L., Babiloni, F., Capotosto, P., Carducci, F., . . . Rossini, P. M. (2004). Alpha event-related desynchronization preceding a go/no-go task: a high-resolution EEG study. *Neuropsychol*, 18(4), 719-728. doi:10.1037/0894-4105.18.4.719

Babiloni, C., Brancucci, A., Del Percio, C., Capotosto, P., Arendt-Nielsen, L., Chen, A., & Rossini, P. M. (2006). Anticipatory electroencephalography alpha rhythm predicts subjective perception of pain intensity. *J Pain, 7*(10), 709-717.

Bahrick, H. P., Fitts, P. M., & Rankin, R. E. (1952). Effect of incentives upon reactions to peripheral stimuli. *J Exp Psychol, 44*(6), 400-406. doi:10.1037/h0053593

Baker, S. N. (2007). Oscillatory interactions between sensorimotor cortex and the periphery. *Curr Opin Neurobiol, 17*(6), 649-655. doi:10.1016/j.conb.2008.01.007

Baker, S. N., Kilner, J. M., Pinches, E. M., & Lemon, R. N. (1999). The role of synchrony and oscillations in the motor output. *Exp Brain Res, 128*(1-2), 109-117. doi:10.1007/s002210050825

Baker, S. N., Olivier, E., & Lemon, R. N. (1997). Coherent oscillations in monkey motor cortex and hand muscle emg show task-dependent modulation. *J Physiol, 501*(1), 225-241. doi:10.1111/j.1469-7793.1997.225bo.x

Balconi, M., Finocchiaro, R., & Canavesio, Y. (2014). Reward-system effect (BAS rating), left hemispheric “unbalance”(alpha band oscillations) and decisional impairments in drug addiction. *Addict Behav*, 39(6), 1026-1032. doi: 10.1016/j.addbeh.2014.02.007

Balconi, M., & Mazza, G. (2009). Brain oscillations and BIS/BAS (behavioral inhibition/activation system) effects on processing masked emotional cues.: ERS/ERD and coherence measures of alpha band. *Int J Psychophysiol*, 74(2), 158-165.

Balodis, I. M., & Potenza, M. N. (2015). Anticipatory reward processing in addicted populations: a focus on the monetary incentive delay task. *Biol Psychiatry, 77*(5), 434-444. doi:10.1016/j.biopsych.2014.08.020

Band, & Logan, G. (2003). Horse-race model simulations of the stop-signal procedure. *Acta Psychol, 112*(2), 105-142. doi:10.1016/S0001-6918(02)00079-3

Band, G. P., Van Der Molen, M. W., & Logan, G. D. (2003). Horse-race model simulations of the stop-signal procedure. *Acta psychologica, 112*(2), 105-142.

Bandura, A. (1977). Self-efficacy: toward a unifying theory of behavioral change. *Psychol Rev*, 84(2), 191-215. doi:10.1037//0033-295x.84.2.191

Bandura, A. (1991). Anticipatory and self-reactive mechanisms. paper presented at the Nebraska symposium on motivation, perspectives on motivation.

Bandura, A., & Cervone, D. (1983). Self-evaluative and self-efficacy mechanisms governing the motivational effects of goal systems. *J Person Soc Psychol*, 45(5), 1017. doi:10.1037/0022-3514.45.5.1017

Bardgett, M. E., Depenbrock, M., Downs, N., Points, M., & Green, L. (2009). Dopamine modulates effort-based decision making in rats. *Behav Neurosci, 123*(2), 242-251. doi:10.1037/a0014625

Bardouille, T., & Bailey, L. (2019). Evidence for age-related changes in sensorimotor neuromagnetic responses during cued button pressing in a large open-access dataset. *Neuroimage*, 193, 25-34. doi:10.1016/j.neuroimage.2019.02.065

Bargh, J. A., Chaiken, S., Raymond, P., & Hymes, C. (1996). The automatic evaluation effect: unconditional automatic attitude activation with a pronunciation task. *J Exp Soc Psychol,* 32(1), 104-128. doi:10.1006/jesp.1996.0005

Bartholdy, S., Dalton, B., O'Daly, O. G., Campbell, I. C., & Schmidt, U. (2016). A systematic review of the relationship between eating, weight and inhibitory control using the stop signal task. *Neurosci Biobehav Rev, 64*, 35-62. doi:10.1016/j.neubiorev.2016.02.010

Bartra, O., McGuire, J. T., & Kable, J. W. (2013). The Valuation System: A Coordinate-Based Meta-Analysis of BOLD fMRI Experiments Examining Neural Correlates of Subjective Value. *Neuroimage, 76*, 412-427. doi:10.1016/j.neuroimage.2013.02.063

Barwick, F., Arnett, P., & Slobounov, S. (2012). EEG correlates of fatigue during administration of a neuropsychological test battery. Clin Neurophysiol, 123(2), 278-284. doi:10.1016/j.clinph.2011.06.027

Basar-Eroglu, C., Basar, E., Demiralp, T., & Schurmann, M. (1992). P300-response: possible psychophysiological correlates in delta and theta frequency channels. A review. *Int J Psychophysiol, 13*(2), 161-179.

Basar, E. (1976). *Biophysical and physiological systems analysis*. Boston, U.S: Addison-Wesley Pub. Co., Advanced Book Program.

Başar, E., & Bullock, T. H. (1992). *Induced rhythms in the brain*. Berlin, Germany: Springer.

Başar, E., & Weiss, C. (1981). *Vasculature and circulation: the role of myogenic reactivity in the regulation of blood flow*. Amsterdam, Netherlands: Elsevier-North-Holland Biomedical Press.

Basner, M., & Dinges, D. F. (2011). Maximizing sensitivity of the psychomotor vigilance test (PVT) to sleep loss. *Sleep, 34*(5), 581-591. doi:10.1093/sleep/34.5.581

Bastiaansen, M. C., Böcker, K. B., & Brunia, C. H. (2002). ERd as an index of anticipatory attention? effects of stimulus degradation. *Psychophysiol, 39*(1), 16-28. doi:10.1017/s0048577202000483

Bastiaansen, M. C., Bocker, K. B., Brunia, C. H., de Munck, J. C., & Spekreijse, H. (2001). Event-related desynchronization during anticipatory attention for an upcoming stimulus: a comparative EEG/MEG study. *Clin Neurophysiol, 112*(2), 393-403. doi:10.1016/S1388-2457(00)00537-X

Bauer, M., Kennett, S., & Driver, J. (2012). Attentional selection of location and modality in vision and touch modulates low-frequency activity in associated sensory cortices. *J Neurophysiol, 107*(9), 2342-2351. doi:10.1152/jn.00973.2011

Bauer, M., Oostenveld, R., Peeters, M., & Fries, P. (2006). Tactile spatial attention enhances gamma-band activity in somatosensory cortex and reduces low-frequency activity in parieto-occipital areas. *J Neurosci, 26*(2), 490-501. doi:10.1523/jneurosci.5228-04.2006

Baumeister, Bratslavsky, Finkenauer, & Vohs. (2001). Bad is stronger than good. *Rev Gen Psychol, 5*(4), 323-370. doi:10.1037/1089-2680.5.4.323

Baumeister, R. F. (2002). Yielding to temptation: self-control failure, impulsive purchasing, and consumer behavior. *J Consum Res, 28*(4), 670-676. doi:10.1086/338209

Bayer, U. C., & Gollwitzer, P. M. (2005). Mindset effects on information search in self-evaluation. *J Soc Psychol,* 35(3), 313-327. doi:10.1002/ejsp.247

Beatty, S. E., & Smith, S. M. (1987). External search effort: an investigation across several product categories. *J Consum Res, 14*(1), 83-95. doi:10.1086/209095

Beck, S. M., Locke, H. S., Savine, A. C., Jimura, K., & Braver, T. S. (2010). Primary and secondary rewards differentially modulate neural activity dynamics during working memory. PloS one, 5(2), e9251. doi:10.1371/journal.pone.0009251

Bedard, C., Kroger, H., & Destexhe, A. (2006). Model of low-pass filtering of local field potentials in brain tissue. *Phys Rev E Stat Nonlin Soft Matter Phys, 73*(5 Pt 1), 051911. doi:10.1103/PhysRevE.73.051911

Benedek, M., Bergner, S., Konen, T., Fink, A., & Neubauer, A. C. (2011). EEG Alpha synchronization is related to top-down processing in convergent and divergent thinking. *Neuropsychol, 49*(12), 3505-3511. doi:10.1016/j.neuropsychologia.2011.09.004

Benington, J. H., & Heller, H. C. (1995). Restoration of brain energy metabolism as the function of sleep. *Prog Neurobiol, 45*(4), 347-360. doi:10.1016/0301-0082(94)00057-O

Benoit, C., Solopchuk, O., Borragán, G., Carbonnelle, A., Van Durme, S., & Zénon, A. (2019). Cognitive task avoidance correlates with fatigue-induced

performance decrement but not with subjective fatigue. *Neuropsychologia, 123*, 30-40. doi:10.1016/j.neuropsychologia.2018.06.017

Berchou, R., Chayasirisobhon, S., Green, V., & Mason, K. (1986). The pharmacodynamic properties of lorazepam and methylphenidate drugs on event-related potentials and power spectral analysis in normal subjects. *Clin Electroencephalogr, 17*(4), 176-180.

Berg, P., & Scherg, M. (1994). A multiple source approach to the correction of eye artifacts. *Electroencephalogr Clin Neurophysiol, 90*(3), 229-241. doi:10.1016/0013-4694(94)90094-9

Berger, H. J. (1929). Über das elektrenkephalogramm des menschen. *Archiv für psychiatrie und nervenkrankheiten, 87*(1), 527-570.

Bernat, E. M., Malone, S. M., Williams, W. J., Patrick, C. J., & Iacono, W. G. (2007). Decomposing delta, theta, and alpha time-frequency erp activity from a visual oddball task using PCA. *Int J Psychophysiol, 64*(1), 62-74. doi:10.1016/j.ijpsycho.2006.07.015

Berntson, G. G., Lozano, D. L., Chen, Y. J., & Cacioppo, J. T. (2004). Where to Q in PEP. *Psychophysiol*, 41(2), 333-337. doi:10.1111/j.1469-8986.2004.00156.x

Berridge, K. C. (2007). The debate over dopamine's role in reward: the case for incentive salience. *Psychopharmacol, 191*(3), 391-431. doi:10.1007/s00213-006-0578-x

Besle, J., Schevon, C. A., Mehta, A. D., Lakatos, P., Goodman, R. R., McKhann, G. M., . . . Schroeder, C. E. (2011). Tuning of the human neocortex to the temporal dynamics of attended events. *J Neurosci, 31*(9), 3176-3185. doi:10.1523/jneurosci.4518-10.2011

Bestmann, S., & Duque, J. (2016). Transcranial magnetic stimulation: decomposing the processes underlying action preparation. *Neuroscientist, 22*(4), 392-405. doi:10.1177/1073858415592594

Bhalla, M., & Proffitt, D. R. (1999). Visual-motor recalibration in geographical slant perception. *J Exp Psychol Hum Percept Perform*, 25(4), 1076-1096. doi:10.1037//0096-1523.25.4.1076

Bialaszek, W., Marcowski, P., & Ostaszewski, P. (2017). Physical and cognitive effort discounting across different reward magnitudes: tests of discounting models. *PloS one, 12*(7), e0182353. doi:10.1371/journal.pone.0182353

Białaszek, W., Ostaszewski, P., Green, L., & Myerson, J. (2019). On four types of devaluation of outcomes due to their costs: delay, probability, effort, and social discounting. *Psychol Rec, 69*(3), 415-424. doi:10.1007/s40732-019-00340-x

Bijleveld, E., Custers, R., & Aarts, H. (2010). Unconscious reward cues increase invested effort, but do not change speed-accuracy tradeoffs. *Cogn, 115*(2), 330-335. doi:10.1016/j.cognition.2009.12.012

Binti, A. H., Pike, A. C., & Robinson, O. J. (2021). Threat of shock promotes passive avoidance, but not active avoidance. *Eur J Neurosci*. doi:10.1111/ejn.15184

Birnberg, J. G., Luft, J., & Shields, M. D. (2006). Psychology theory in management accounting research. *Handb Manag Account Res, 1*, 113-135. doi:10.1016/S1751-3243(06)01004-2

Bitgood, S., & Dukes, S. (2006). Not another step! economy of movement and pedestrian choice point behavior in shopping malls. *Environ Behav, 38*(3), 394-405. doi:10.1016/S1751-3243(06)01004-2

Blackman, R. B., & Tukey, J. W. (1958). The measurement of power spectra from the point of view of communications engineering—part I. *Bell Syst Tech J*, 37(1), 185-282. doi:10.1002/j.1538-7305.1958.tb03874.x

Blain, B., Hollard, G., & Pessiglione, M. (2016). Neural mechanisms underlying the impact of daylong cognitive work on economic decisions. *Proc Natl Acad Sci, 113*(25), 6967-6972. doi:10.1073/pnas.1520527113

Blair, R. C., & Karniski, W. (1993). An alternative method for significance testing of waveform difference potentials. *Psychophysiol, 30*(5), 518-524. doi:10.1111/j.1469-8986.1993.tb02075.x

Blau, G. (1993). Operationalizing direction and level of effort and testing their relationships to individual job performance. *Organ Behav Hum Decis Proc, 55*(1), 152-170. doi:10.1006/obhd.1993.1028

Block, R. A., Hancock, P. A., & Zakay, D. (2016). Physical load affects duration judgments: A meta-analytic review. *Acta Psychol (Amst)*, 165, 43-47. doi:10.1016/j.actpsy.2016.01.002

Boehler, C. N., Hopf, J. M., Stoppel, C. M., & Krebs, R. M. (2012). Motivating inhibition - reward prospect speeds up response cancellation. *Cogn*, 125(3), 498-503. doi:10.1016/j.cognition.2012.07.018

Boehler, C. N., Schevernels, H., Hopf, J. M., Stoppel, C. M., & Krebs, R. M. (2014). Reward prospect rapidly speeds up response inhibition via reactive control. *Cogn Affect Behav Neurosci, 14*(2), 593-609. doi:10.3758/s13415-014-0251-5

Boeijinga, P. H., Parot, P., Soufflet, L., Landron, F., Danel, T., Gendre, I., . . . Luthringer, R. (2004). Pharmacodynamic effects of acamprosate on markers of cerebral function in alcohol-dependent subjects administered as

pretreatment and during alcohol abstinence. *Neuropsychobiol, 50*(1), 71-77. doi:10.1159/000077944

Bogacz, R., Brown, E., Moehlis, J., Holmes, P., & Cohen, J. D. (2006). The physics of optimal decision making: a formal analysis of models of performance in two-alternative forced-choice tasks. *Psychol Rev, 113*(4), 700-765. doi:10.1037/0033-295x.113.4.700

Boiten, F., Sergeant, J., & Geuze, R. (1992). Event-related desynchronization: the effects of energetic and computational demands. *Electroencephalogr Clin Neurophysiol, 82*(4), 302-309. doi:10.1016/0013-4694(92)90110-4

Boksem, M. A., & Tops, M. (2008). Mental Fatigue: Costs and Benefits. *Brain Res Rev*, 59(1), 125-139. doi:10.1016/j.brainresrev.2008.07.001

Boksem, M. A., & Tops, M. (2008). Mental fatigue: costs and benefits. *Brain Res Rev, 59*(1), 125-139. doi:10.1016/j.brainresrev.2008.07.001

Boksem, M. A., Tops, M., Kostermans, E., & De Cremer, D. (2008). Sensitivity to punishment and reward omission: evidence from error-related ERP components. *Biol Psychol, 79*(2), 185-192. doi:10.1016/j.biopsycho.2008.04.010

Bokura, H., Yamaguchi, S., & Kobayashi, S. (2001). Electrophysiological correlates for response inhibition in a Go/NoGo task. *Clin Neurophysiol, 112*(12), 2224-2232. doi:10.1016/s1388-2457(01)00691-5

Bonnefond, M., & Jensen, O. (2012). Alpha oscillations serve to protect working memory maintenance against anticipated distracters. *Curr Biol, 22*(20), 1969-1974. doi:10.1016/j.cub.2012.08.029

Bonner, S. E., Hastie, R., Sprinkle, G. B., & Young, S. M. (2000). A review of the effects of financial incentives on performance in laboratory tasks:

implications for management accounting. *J Management Account Res, 12*(1), 19-64. doi:10.2308/jmar.2000.12.1.19

Bonvallet, M., & Newman-Taylor, A. (1967). Neurophysiological evidence for a differential organization of the mesencephalic reticular formation. *Electroencephalogr Clin Neurophysiol, 22*(1), 54-73.

Boska, M. (1994). ATP production rates as a function of force level in the human gastrocnemius/soleus using 31P MRS. *Magn Reson Med,* 32(1), 1-10. doi:10.1002/mrm.1910320102

Bossaerts, P., & Murawski, C. (2015). From behavioural economics to neuroeconomics to decision neuroscience: the ascent of biology in research on human decision making. *Current Opinion in Behavioral Sciences, 5*, 37-42. doi:10.1016/j.cobeha.2015.07.001

Botvinick, M. M. (2007). Conflict monitoring and decision making: reconciling two perspectives on anterior cingulate function. *Cogn Affect Behav Neurosci, 7*(4), 356-366. doi:10.3758/cabn.7.4.356

Botvinick, M. M., & Braver, T. (2015). Motivation and cognitive control: from behavior to neural mechanism. *Annu Rev Psychol, 66*, 83-113. doi:10.1146/annurev-psych-010814-015044

Botvinick, M. M., Braver, T. S., Barch, D. M., Carter, C. S., & Cohen, J. D. (2001). Conflict monitoring and cognitive control. *Psychol Rev, 108*(3), 624. doi:10.1037/0033-295X.108.3.624

Botvinick, M. M., & Cohen, J. D. (2014). The computational and neural basis of cognitive control: charted territory and new frontiers. *Cogn Sci, 38*(6), 1249-1285. doi:10.1111/cogs.12126

Botvinick, M. M., Cohen, J. D., & Carter, C. S. (2004). Conflict monitoring and anterior cingulate cortex: an update. *Trends Cogn Sci, 8*(12), 539-546. doi:10.1016/j.tics.2004.10.003

Botvinick, M. M., Niv, Y., & Barto, A. C. (2009). Hierarchically organized behavior and its neural foundations: a reinforcement learning perspective. *Cogn, 113*(3), 262-280. doi:10.1016/j.cognition.2008.08.011

Bötzel, K., Ecker, C., & Schulze, S. (1997). Topography and dipole analysis of reafferent electrical brain activity following the Bereitschaftspotential. *Exp Brain Res,* 114(2), 352-361. doi:10.1007/pl00005643

Boureau, Y. L., & Dayan, P. (2011). Opponency revisited: competition and cooperation between dopamine and serotonin. *Neuropsychopharmacol, 36*(1), 74-97. doi:10.1038/npp.2010.151

Bradley, M. M., Codispoti, M., Cuthbert, B. N., & Lang, P. J. (2001). Emotion and motivation i: defensive and appetitive reactions in picture processing. *Emotion, 1*(3), 276-298. doi:10.1037/1528-3542.1.3.276

Bradley, M. M., & Lang, P. J. (1999). *Affective norms for English words (ANEW): Instruction manual and affective ratings*. Retrieved from university of florida:

bradley, m. m., & lang, p. j. (2000). measuring emotion: behavior, feeling, and physiology. *Cogn Neurosci of Emot, 25*, 49-59.

Brain, P. F. (1999). The role of biological factors. In *Handbook of Psychological Approaches with Violent Offenders* (pp. 83-92). Bern, Swizerland: Springer.

Brandstätter, V., Giesinger, L., Job, V., & Frank, E. (2015). The role of deliberative versus implemental mindsets in time prediction and task accomplishment. *Soc Psychol,* 46(2), 104. doi:10.1027/1864-9335/a000231

Braver, T. S., & Cohen, J. D. (2000). On the control of control: the role of dopamine in regulating prefrontal function and working memory. *MIT Press*, 713-737.

Braver, T. S. (2012). The variable nature of cognitive control: a dual mechanisms framework. *Trends Cogn Sci*, 16(2), 106-113. doi:10.1016/j.tics.2011.12.010

Brehm, J., W., & Self, E., A. (1989). The intensity of motivation. *Ann Rev Psychol*, 40(1), 109-131. doi:10.1146/annurev.ps.40.020189

Brehm, J. W., & Self, E. A. (1989). The intensity of motivation. *Annu Rev Psychol*, 40, 109-131. doi:10.1146/annurev.ps.40.020189.000545

Bridgeman, B. (2006). Contributions of lateral inhibition to object substitution masking and attention. *Vision Res, 46*(24), 4075-4082. doi:10.1016/j.visres.2006.08.012

Brinkmann, K., & Gendolla, G. H. (2008). Does depression interfere with effort mobilization? Effects of dysphoria and task difficulty on cardiovascular response. *J Pers Soc Psychol*, 94(1), 146-157. doi:10.1037/0022-3514.94.1.146

Bromberg-Martin, E. S., Matsumoto, M., & Hikosaka, O. (2010). Dopamine in motivational control: rewarding, aversive, and alerting. *Neuron*, 68(5), 815-834. doi:10.1016/j.neuron.2010.11.022

Brooks, R. R., Stremitzer, A., & Tontrup, S. (2017). Stretch it but don't break it: the hidden cost of contract framing. *J Leg Stud*, *46*(2), 399-426. doi:10.1086/694234

Brovelli, A., Ding, M., Ledberg, A., Chen, Y., Nakamura, R., & Bressler, S. L. (2004). Beta oscillations in a large-scale sensorimotor cortical network: directional influences revealed by granger causality. *Proc Natl Acad Sci, 101*(26), 9849-9854. doi:10.1073/pnas.0308538101

Brown, G. G., Kindermann, S. S., Siegle, G. J., Granholm, E., Wong, E. C., & Buxton, R. B. (1999). Brain activation and pupil response during covert performance of the Stroop Color Word task. *J Int Neuropsychol Soc*, 5(4), 308-319. doi:10.1017/s1355617799544020

Brunel, N., & Wang, X. J. (2003). What determines the frequency of fast network oscillations with irregular neural discharges? *J Neurophysiol*, *90*(1), 415-430. doi:10.1152/jn.01095.2002

Bu, X., Liu, Y., Wang, Q., Jiao, S., Zeng, F., Yao, X., . . . Wang, Y. (2015). Serum amyloid-beta levels are increased in patients with obstructive sleep apnea syndrome. *Sci Rep, 5*, 13917. doi:10.1038/srep13917

Bullmore, E., Brammer, M., Williams, S. C., Rabe-Hesketh, S., Janot, N., David, A., . . . Sham, P. (1996). Statistical methods of estimation and inference for functional mr image analysis. *Magn Reson Med, 35*(2), 261-277. doi:10.1002/mrm.1910350219

Bullmore, E. T., Suckling, J., Overmeyer, S., Rabe-Hesketh, S., Taylor, E., & Brammer, M. J. (1999). Global, voxel, and cluster tests, by theory and permutation, for a difference between two groups of dtructural mr images of the brain. *IEEE Trans Med Imaging, 18*(1), 32-42. doi:10.1109/42.750253

Burke, C. J., Brunger, C., Kahnt, T., Park, S. Q., & Tobler, P. N. (2013). Neural integration of risk and effort costs by the frontal pole: only upon request. *J Neurosci, 33*(4), 1706-1713a. doi:10.1523/jneurosci.3662-12.2013

Busch, N. A., & VanRullen, R. (2010). Spontaneous EEG oscillations reveal periodic sampling of visual attention. *Proc Natl Acad Sci 107*(37), 16048-16053. doi:10.1073/pnas.1004801107

Buchsbaum, M. S., Nuechterlein, K. H., Haier, R. J., Wu, J., Sicotte, N., Hazlett, E., . . . Guich, S. (1990). Glucose metabolic rate in normals and schizophrenics during the continuous performance test assessed by positron emission tomography. *Br J Psychiatry*, 156, 216-227. doi:10.1192/bjp.156.2.216

Buschman, T. J., & Miller, E. K. (2007). Top-down versus bottom-up control of attention in the prefrontal and posterior parietal cortices. *Sci, 315*(5820), 1860-1862. doi:10.1126/science.1138071

Buschman, T. J., & Miller, E. K. (2009). Serial, covert shifts of attention during visual search are reflected by the frontal eye fields and correlated with population oscillations. *Neuron, 63*(3), 386-396. doi:10.1016/j.neuron.2009.06.020

Büttner, O. B., Wieber, F., Schulz, A. M., Bayer, U. C., Florack, A., & Gollwitzer, P. M. (2014). Visual attention and goal pursuit: deliberative and implemental mindsets affect breadth of attention. *Pers Soc Psychol Bull,* 40(10), 1248-1259. doi:10.1177/0146167214539707

Button, K. S., Ioannidis, J. P., Mokrysz, C., Nosek, B. A., Flint, J., Robinson, E. S., & Munafo, M. R. (2013). Power failure: why small sample size undermines the reliability of neuroscience. *Nat Rev Neurosci, 14*(5), 365-376. doi:10.1038/nrn3475

Buzsáki, G., & Draguhn, A. (2004). Neuronal oscillations in cortical networks. *Sci, 304*(5679), 1926-1929. doi:10.1126/science.1099745

Buzy, W. M., Medoff, D. R., & Schweitzer, J. B. (2009). Intra-individual variability among children with adhd on a working memory task: an ex-gaussian approach. *Child Neuropsychol, 15*(5), 441-459. doi:10.1080/09297040802646991

Buzzell, G. A., Beatty, P. J., Paquette, N. A., Roberts, D. M., & McDonald, C. G. (2017). Error-induced blindness: error detection leads to impaired sensory processing and lower accuracy at short response-stimulus intervals. *J Neurosci, 37*(11), 2895-2903. doi:10.1523/jneurosci.1202-16.2017

Byrne, A., Hewitt, D., Henderson, J., Newton-Fenner, A., Roberts, H., Tyson-Carr, J., . . . Stancak, A. (Submitted). Changes in anticipatory ERD during an effortful task when incentivised with a gain or loss. *J Psychophysiol.*

Byrne, A., Kokmotou, K., Roberts, H., Soto, V., Tyson-Carr, J., Hewitt, D., . . . Stancak, A. (2020). The cortical oscillatory patterns associated with varying levels of reward during an effortful vigilance task. *Exp Brain Res*, 238(9), 1839-1859. doi:10.1007/s00221-020-05825-8

Byrne, Z. S., Stoner, J., Thompson, K. R., & Hochwarter, W. (2005). The interactive effects of conscientiousness, work effort, and psychological climate on job performance. *J Vocat Behav, 66*(2), 326-338. doi:10.1016/j.jvb.2004.08.005

Byun, T. M., & Hitchcock, E. R. (2012). Investigating the use of traditional and spectral biofeedback approaches to intervention for/r/misarticulation. *Amer J Spe-Lan Pathol*. doi:10.1044/1058-0360(2012/11-0083

Cabanac, M. (1971). Physiological role of pleasure. *Sci, 173*(4002), 1103-1107. doi:10.1126/science.173.4002.1103

Cacioppo, J. T., & Berntson, G. G. (1994). Relationship between attitudes and evaluative space: a critical review, with emphasis on the separability of positive and negative substrates. *Psychol Bull, 115*(3), 401. doi:10.1037/0033-2909.115.3.401

Cacioppo, J. T., Petty, R. E., Feinstein, J. S., & Jarvis, W. (1996). Dispositional differences in cognitive motivation: the life and times of individuals varying in need for cognition. *Psychological bulletin, 119*(2), 197.

Cai, W., Oldenkamp, C. L., & Aron, A. R. (2011). A proactive mechanism for selective suppression of response tendencies. *J Neurosci*, 31(16), 5965-5969. doi: 10.1523/JNEUROSCI.6292-10.2011

Cai, W., Ryali, S., Chen, T., Li, C. S., & Menon, V. (2014). Dissociable roles of right inferior frontal cortex and anterior insula in inhibitory control: evidence from intrinsic and task-related functional parcellation, connectivity, and response profile analyses across multiple datasets. *J Neurosci, 34*(44), 14652-14667. doi:10.1523/jneurosci.3048-14.2014

Camerer, C. F., & Hogarth, R. M. (1999). The effects of financial incentives in experiments: a review and capital-labor-production framework. *J Risk Uncertain, 19*(1-3), 7-42. doi:10.1023/A:1007850605129

Campos, J. J., Bertenthal, B. I., & Kermoian, R. (1992). *Early experience and emotional development: the emergence of wariness of heights*. In. Los Angeles, CA: SAGE Publications.

Capa, R. L., Audiffren, M., & Ragot, S. (2008). The effects of achievement motivation, task difficulty, and goal difficulty on physiological, behavioral, and subjective effort. *Psychophysiol, 45*(5), 859-868. doi:10.1111/j.1469-8986.2008.00675.x

Capotosto, P., Babiloni, C., Romani, G. L., & Corbetta, M. (2009). Frontoparietal cortex controls spatial attention through modulation of anticipatory alpha rhythms. *J Neurosci, 29*(18), 5863-5872. doi:10.1523/jneurosci.0539-09.2009

Carp, J., & Compton, R. J. (2009). Alpha power is influenced by performance errors. *Psychophysiol, 46*(2), 336-343. doi:10.1111/j.1469-8986.2008.00773.x

Carsten, T., Hoofs, V., Boehler, C. N., & Krebs, R. M. (2018). Are losses more effective than rewards in improving performance in a cognitive task? *Motiv Sci*. doi:10.1037/mot0000117

Carter, R. M., Macinnes, J. J., Huettel, S. A., & Adcock, R. A. (2009). Activation in the VTA and nucleus accumbens increases in anticipation of both gains and losses. *Front Behav Neurosci*, 3, 21. doi:10.3389/neuro.08.021.2009

Cassim, F., Monaca, C., Szurhaj, W., Bourriez, J. L., Defebvre, L., Derambure, P., & Guieu, J. D. (2001). Does post-movement beta synchronization reflect an idling motor cortex? *Neuroreport, 12*(17), 3859-3863. doi:10.1097/00001756-200112040-00051

Cassim, F., Szurhaj, W., Sediri, H., Devos, D., Bourriez, J., Poirot, I., . . . Guieu, J. (2000). Brief and sustained movements: differences in event-related (de)synchronization (ERD/ERS) patterns. *Clin Neurophysiol, 111*(11), 2032-2039. doi:10.1016/s1388-2457(00)00455-7

Catania, A. C. (1963). Concurrent performances: a baseline for the study of reinforcement magnitude. *J Exp Anal Behav, 6*(2), 299-300. doi:10.1901/jeab.1963.6-299

Cavanagh, J. F., Cohen, M. X., & Allen, J. J. (2009). Prelude to and resolution of an error: EEG phase synchrony reveals cognitive control dynamics during action monitoring. *J Neurosci, 29*(1), 98-105.

Cavanagh, J. F., & Frank, M. J. (2014). Frontal theta as a mechanism for cognitive control. Trends Cogn Sci, 18(8), 414-421. doi:10.1016/j.tics.2014.04.012

Cavanagh, J. F., Frank, M. J., Klein, T. J., & Allen, J. J. (2010). Frontal theta links prediction errors to behavioral adaptation in reinforcement learning. *Neuroimage, 49*(4), 3198-3209. doi:10.1016/j.neuroimage.2009.11.080

Cavanagh, J. F., Zambrano-Vazquez, L., & Allen, J. J. (2012). Theta lingua franca: a common mid-frontal substrate for action monitoring processes. *Psychophysiol, 49*(2), 220-238. doi:10.1111/j.1469-8986.2011.01293.x

Cedernaes, J., Osorio, R. S., Varga, A. W., Kam, K., Schiöth, H. B., & Benedict, C. (2017). Candidate mechanisms underlying the association between sleep-wake disruptions and alzheimer's disease. *Sleep Med Rev, 31*, 102-111. doi:10.1016/j.smrv.2016.02.002

Chakravarthi, R., & Vanrullen, R. (2012). Conscious updating is a rhythmic process. *Proc Natl Acad Sci 109*(26), 10599-10604. doi:10.1073/pnas.1121622109

Chambers, C. D., Payne, J. M., Stokes, M. G., & Mattingley, J. B. (2004). Fast and slow parietal pathways mediate spatial attention. *Nat Neurosci, 7*(3), 217-218. doi:10.1038/nn1203

Chao, L. L., & Knight, R. T. (1995). Human prefrontal lesions increase distractibility to irrelevant sensory inputs. *Neuroreport, 6*(12), 1605-1610.

Chapman, C. E. (1996). Temporal discounting and utility for health and money. *J Exp Psychol Learn Mem Cogn, 22*(3), 771-791. doi:10.1037//0278-7393.22.3.771

Chapman, C. E., Gallivan, J. P., Wong, J. D., Wispinski, N. J., & Enns, J. T. (2015). The snooze of lose: rapid reaching reveals that losses are processed more slowly than gains. *J Exp Psychol Gen, 144*(4), 844-863. doi:10.1037/xge0000085

Chatrian, G. E., Petersen, M. C., & Lazarte, J. A. (1959). The blocking of the rolandic wicket rhythm and some central changes related to movement. *Electroencephalogr Clin Neurophysiol, 11*(3), 497-510. doi:10.1016/0013-4694(59)90048-3

Chatterjee, A., Aggarwal, V., Ramos, A., Acharya, S., & Thakor, N. V. (2007). A brain-computer interface with vibrotactile biofeedback for haptic information. *J Neuro Rehab*, 4(1), 40. doi:10.1186/1743-0003-4-40

Cheignon, C., Tomas, M., Bonnefont-Rousselot, D., Faller, P., Hureau, C., & Collin, F. (2018). Oxidative stress and the amyloid beta peptide in alzheimer's Disease. *Redox Biol, 14*, 450-464. doi:10.1016/j.redox.2017.10.014

Chen, M., & Bargh, J. A. (1999). Consequences of automatic evaluation: immediate behavioral predispositions to approach or avoid the stimulus. *Personal Soc Psychol Bull*, 25(2), 215-224. doi: 10.1177/0146167299025002007

Chen, A., Chen, C. Y., Wang, Y., & He, G. (2019). Probability discounting of environmental gains: do we multiply or add up? *J Risk Res, 22*(12), 1479-1489. doi:10.1080/13669877.2018.1485167

Chen, A., Lakshminarayanan, V., & Santos, L. R. (2006). How basic are behavioral biases? evidence from capuchin monkey trading behavior. *J Pol Econ, 114*(3), 517-537. doi:10.1086/503550

Chen, A., Yaseen, Z., Cohen, L. G., & Hallett, M. (1998). Time course of corticospinal excitability in reaction time and self-paced movements. *Annal of Neurol, 44*(3), 317-325. doi: 10.1002/ana.410440306

Chevrier, A. D., Noseworthy, M. D., & Schachar, R. (2007). Dissociation of response inhibition and performance monitoring in the stop signal task using

event-related fMRI. *Hum Brain Mapp, 28*(12), 1347-1358. doi:10.1002/hbm.20355

Chiu, Y. C., Cools, R., & Aron, A. R. (2014). Opposing effects of appetitive and aversive cues on Go/No-Go behavior and motor excitability. *J Cogn Neurosci*, 26(8), 1851-1860. doi:10.1162/jocn_a_00585

Choi, J. M., Padmala, S., Spechler, P., & Pessoa, L. (2014). Pervasive competition between threat and reward in the brain. *Soc Cogn Affect Neurosci*, 9(6), 737-750. doi:10.1093/scan/nst053

Chong, T. T., Apps, M., Giehl, K., Sillence, A., Grima, L. L., & Husain, M. (2017). Neurocomputational mechanisms underlying subjective valuation of effort costs. *PLoS Biol, 15*(2). doi:10.1371/journal.pbio.1002598

Chow, C. W., Kohlmeyer, J. M., & Wu, A. (2007). Performance standards and managers' adoption of risky projects. In *Adv Manag Account* (pp. 63-105): Emerald Group Publishing Limited.

Chowdhury, R. A., Zerouali, Y., Hedrich, T., Heers, M., Kobayashi, E., Lina, J. M., & Grova, C. (2015). MEG-EEG information fusion and electromagnetic source imaging: from theory to clinical application in epilepsy. *Brain Topogr, 28*(6), 785-812. doi:10.1007/s10548-015-0437-3

Christ, M. H., Sedatole, K. L., & Towry, K. L. (2012). Sticks and carrots: the effect of contract frame on effort in incomplete contracts. *Account Rev, 87*(6), 1913-1938. doi:10.2308/accr-50219

Christie, S. T., & Schrater, P. (2015). Cognitive cost as dynamic allocation of energetic resources. *Front Neurosci, 9*, 289. doi:10.3389/fnins.2015.00289

Church, B. K., Libby, T., & Zhang, P. (2008). Contracting frame and individual behavior: experimental evidence. *J Manag Account Res, 20*(1), 153-168. doi:10.2308/jmar.2008.20.1.153

Clarke, K., & Belk, R. W. (1979). The effects of product involvement and task definition on anticipated consumer effort. *Advance Cons Res, 06*.

Clithero, J. A., & Rangel, A. (2014). Informatic parcellation of the network involved in the computation of subjective value. *Soc Cogn Affect Neurosci, 9*(9), 1289-1302. doi:10.1093/scan/nst106

Cohen, J. D., & Cuffin, B. N. (1991). EEG versus MEG localization accuracy: theory and experiment. *Brain Topogr, 4*(2), 95-103. doi:10.1007/BF01132766

Cohen, J. D., Dunbar, K., & McClelland, J. L. (1990). On the control of automatic processes: a parallel distributed processing account of the Stroop effect. *Psychol Rev, 97*(3), 332-361. doi:10.1037/0033-295x.97.3.332

Cohen, J. D., Lohr, I., Paul, R., & Boland, R. (2001). Impairments of attention and effort among patients with major affective disorders. *J Neuropsych Clin Neurosci, 13*(3), 385-395. doi:10.1176/jnp.13.3.385

Cohen, J. D., & Ranganath, C. (2007). Reinforcement learning signals predict future decisions. *J Neurosci, 27*(2), 371-378. doi:10.1523/jneurosci.4421-06.2007

Cohen, J. D., & Servan-Schreiber, D. (1992). Context, cortex, and dopamine: a connectionist approach to behavior and biology in schizophrenia. *Psychol Rev, 99*(1), 45-77. doi:10.1037/0033-295X.99.1.45

Cohen, M. X. (2017). Rigor and replication in time-frequency analyses of cognitive electrophysiology data. *Int J Psychophysiol*, 111, 80-87. doi:10.1016/j.ijpsycho.2016.02.001

Colebatch, J. G., Deiber, M. P., Passingham, R. E., Friston, K. J., & Frackowiak, R. S. (1991). Regional cerebral blood flow during voluntary arm and hand movements in human subjects. *J Neurophysiol, 65*(6), 1392-1401. doi:10.1152/jn.1991.65.6.1392

Collette, F., Schmidt, C., Scherrer, C., Adam, S., & Salmon, E. (2009). Specificity of inhibitory deficits in normal aging and Alzheimer's disease. *Neurobiol Aging, 30*(6), 875-889. doi:10.1016/j.neurobiolaging.2007.09.007

Combes, J.-M., Grossmann, A., & Tchamitchian, P. (2012). Wavelets: time-frequency methods and phase space proceedings of the international conference, Marseille, France, December 14–18, 1987: Springer Science & Business Media.

Connemann, B. J., Mann, K., Lange-Asschenfeldt, C., Ruchsow, M., Schreckenberger, M., Bartenstein, P., & Gründer, G. (2005). Anterior limbic alpha-like activity: a low resolution electromagnetic tomography study with lorazepam challenge. *Clin Neurophysiol, 116*(4), 886-894. doi:10.1016/j.clinph.2004.11.015

Conway, B. A., Halliday, D. M., Farmer, S. F., Shahani, U., Maas, P., Weir, A. I., & Rosenberg, J. R. (1995). Synchronization between motor cortex and spinal motoneuronal pool during the performance of a maintained motor task in man. *J Physiol, 489 (Pt 3)*(Pt 3), 917-924. doi:10.1113/jphysiol.1995.sp021104

Cools, R. (2016). The costs and benefits of brain dopamine for cognitive control. *Wiley Interdiscip Rev Cogn Sci, 7*(5), 317-329. doi:10.1002/wcs.1401

Cools, R., Clark, L., Owen, A. M., & Robbins, T. W. (2002). Defining the neural mechanisms of probabilistic reversal learning using event-related functional magnetic resonance imaging. *J Neurosci, 22*(11), 4563-4567. doi:20026435

Cools, R., & D'Esposito, M. (2011). Inverted-U-shaped dopamine actions on human working memory and cognitive control. *Biol Psychiatry, 69*(12), e113-125. doi:10.1016/j.biopsych.2011.03.028

Cools, R., Nakamura, K., & Daw, N. D. (2011). Serotonin and dopamine: unifying affective, activational, and decision functions. *Neuropsychopharmacol, 36*(1), 98-113. doi:10.1038/npp.2010.121

Corbetta, M., Kincade, J. M., Ollinger, J. M., McAvoy, M. P., & Shulman, G. L. (2000). Voluntary orienting is dissociated from target detection in human posterior parietal cortex. *Nat Neurosci, 3*(3), 292-297. doi:10.1038/73009

Corbetta, M., Patel, G., & Shulman, G. L. (2008). The reorienting system of the human brain: from environment to theory of mind. *Neuron, 58*(3), 306-324. doi:10.1016/j.neuron.2008.04.017

Corbetta, M., & Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nat Rev Neurosci, 3*(3), 201-215. doi:10.1038/nrn755

Coull, J. T., Walsh, V., Frith, C. D., & Nobre, A. C. (2003). Distinct neural substrates for visual search amongst spatial versus temporal distractors. *Brain Res Cogn Brain Res, 17*(2), 368-379. doi:10.1016/s0926-6410(03)00138-1

Coxon, J. P., Stinear, C. M., & Byblow, W. D. (2006). Intracortical inhibition during volitional inhibition of prepared action. *J Neurophysiol, 95*(6), 3371-3383. doi:10.1152/jn.01334.2005

Craig, A. D. (2002). How do you feel? Interoception: the sense of the physiological condition of the body. *Nat Rev Neurosci,* 3(8), 655-666. doi:10.1038/nrn894

Craig, A. D. (2009). How do you feel--now? The anterior insula and human awareness. *Nat Rev Neurosci*, 10(1), 59-70. doi:10.1038/nrn2555

Cravo, A. M., Rohenkohl, G., Wyart, V., & Nobre, A. C. (2013). Temporal expectation enhances contrast sensitivity by phase entrainment of low-frequency oscillations in visual cortex. *J Neurosci, 33*(9), 4002-4010. doi:10.1523/jneurosci.4675-12.2013

Cremoux, S., Tallet, J., Berton, E., Dal Maso, F., & Amarantini, D. (2013). Motor-related cortical activity after cervical spinal cord injury: multifaceted eeg analysis of isometric elbow flexion contractions. *Brain Res, 1533*, 44-51. doi:10.1016/j.brainres.2013.08.008

Creutzfeldt, O., Grünewald, G., Simonova, O., & Schmitz, H. (1969). Changes of the basic rhythms of the eeg during the performance of mental and visuomotor tasks. In *Attention in neurophysiology* (pp. 148-168). London, UK: Butterworths.

Critchley, H. D., Mathias, C. J., Josephs, O., O'Doherty, J., Zanini, S., Dewar, B. K., . . . Dolan, R. J. (2003). Human cingulate cortex and autonomic control: converging neuroimaging and clinical evidence. *Brain, 126*(10), 2139-2152. doi:10.1093/brain/awg216

Crone, N. E., Miglioretti, D. L., Gordon, B., Sieracki, J. M., Wilson, M. T., Uematsu, S., & Lesser, R. P. (1998). Functional mapping of human sensorimotor cortex with electrocorticographic spectral analysis. *Brain, 121 (Pt 12)*, 2271-2299. doi:10.1093/brain/121.12.2271

Csibra, G., & Johnson, M. W. (2013). Investigating event-related oscillations in infancy. I*nfant EEG Event-Relat Potentials*, 289.

Cuevas, K., Cannon, E. N., Yoo, K., & Fox, N. A. (2014). The infant EEG mu rhythm: methodological considerations and best practices. *Dev Rev, 34*(1), 26-43. doi:10.1016/j.dr.2013.12.001

Culbreth, A., Westbrook, A., & Barch, D. (2016). Negative symptoms are associated with an increased subjective cost of cognitive effort. *J Abnorm Psychol, 125*(4), 528-536. doi:10.1037/abn0000153

D'Esposito, M. (2007). From cognitive to neural models of working memory. *Philos Trans R Soc Lond B Biol Sci, 362*(1481), 761-772. doi:10.1098/rstb.2007.2086

Daubechies, I., & Bates, B. J. (1993). Ten lectures on wavelets. doi:10.1063/1.168556

Davidson, R. J., Ekman, P., Saron, C. D., Senulis, J. A., & Friesen, W. V. (1990). Approach-withdrawal and cerebral asymmetry: emotional expression and brain physiology: I. *J Personality Soc Psychol, 58*(2), 330. doi:10.1037/0022-3514.58.2.330

Davis, M. (1989). *The role of the amygdala and its efferent projections in fear and anxiety*. Oxford, UK: Oxford University Press.

Davis, M., Walker, D. L., Miles, L., & Grillon, C. (2010). Phasic vs sustained fear in rats and humans: role of the extended amygdala in fear vs anxiety. *Neuropsychopharmacol*, 35(1), 105-135. doi:10.1038/npp.2009.109

Daw, N. D., O'Doherty, J. P., Dayan, P., Seymour, B., & Dolan, R. J. (2006). Cortical substrates for exploratory decisions in humans. *Nat, 441*(7095), 876-879. doi:10.1038/nature04766

Dawson, M. E., Oray, S., Lu, Z. L., & Schell, A. M. (2004). Prepulse inhibition of event-related brain potentials and startle eyeblink. *Adv Psychol Res, 29*, 57-70.

De Houwer, J., Crombez, G., Baeyens, F., & Hermans, D. (2001). On the generality of the affective simon effect. *Cogni & Emot, 15*(2), 189-206. doi:10.1080/02699930125883

de Morree, H. M., Klein, C., & Marcora, S. M. (2012). Perception of effort reflects central motor command during movement execution. *Psychophysiol*, 49(9), 1242-1253. doi:10.1111/j.1469-8986.2012.01399.x Deecke, L., & Kornhuber, H. H. (2003). Human freedom, reasoned will, and the brain: The Bereitschaftspotential story. In *The Bereitschaftspotential* (pp. 283-320): Springer.

de Zeeuw, P., Aarnoudse-Moens, C., Bijlhout, J., König, C., Post Uiterweer, A., Papanikolau, A., . . . Oosterlaan, J. (2008). Inhibitory performance, response speed, intraindividual variability, and response accuracy in ADHD. *J Am Acad Child Adolesc Psychiatry*, *47*(7), 808-816. doi:10.1097/CHI.0b013e318172eee9

Debener, S., Ullsperger, M., Siegel, M., Fiehler, K., von Cramon, D. Y., & Engel, A. K. (2005). Trial-by-trial coupling of concurrent electroencephalogram and functional magnetic resonance imaging identifies the dynamics of performance monitoring. *J Neurosci*, *25*(50), 11730-11737. doi:10.1523/jneurosci.3286-05.2005

Debruille, J. B. (1998). Knowledge inhibition and N400: a study with words that look like common words. *Brain Lang*, *62*(2), 202-220. doi:10.1006/brln.1997.1904

Dehaene, S., Artiges, E., Naccache, L., Martelli, C., Viard, A., Schurhoff, F., . . . Martinot, J. L. (2003). Conscious and subliminal conflicts in normal subjects and patients with schizophrenia: the role of the anterior cingulate. *Proc Natl Acad Sci 100*(23), 13722-13727. doi:10.1073/pnas.2235214100

Delgado, M. R. (2007). Reward-related responses in the human striatum. *Annals New York Acad Sci, 1104*(1), 70-88. doi:10.1196/annals.1390.002

Dennehy, T. C., Ben-Zeev, A., & Tanigawa, N. (2014). 'Be prepared': an implemental mindset for alleviating social-identity threat. *Br J Soc Psychol*, 53(3), 585-594. doi:10.1111/bjso.12071

Derambure, P., Defebvre, L., Dujardin, K., Bourriez, J. L., Jacquesson, J. M., Destee, A., & Guieu, J. D. (1993). Effect of aging on the spatio-temporal pattern of event-related desynchronization during a voluntary movement. *Electroencephalogr Clin Neurophysiol*, *89*(3), 197-203. doi:10.1016/0168-5597(93)90133-A

Desimone, R., & Duncan, J. (1995). Neural mechanisms of selective visual attention. *Annual Rev Neurosci, 18*(1), 193-222.

Diamond, A. (2013). Executive functions. *Annual Rev Psychol*, *64*, 135-168. doi:10.1146/annurev-psych-113011-143750

Dickinson, A., & Balleine, B. W. (2000). Causal cognition and goal-directed action. *Evol Cogn*, 185.

Dickinson, A., & Dearing, M. F. (1979). Appetitive-aversive interactions and inhibitory processes. *Mechan Learn Mot*, 203-231.

Dimitrijevic, A., Smith, M. L., Kadis, D. S., & Moore, D. R. (2017). Cortical alpha oscillations predict speech intelligibility. *Front Hum Neurosci, 11*, 88. doi:10.3389/fnhum.2017.00088

Ding, L., & Yuan, H. (2013). Simultaneous EEG and MEG source reconstruction in sparse electromagnetic source imaging. *Hum Brain Mapp, 34*(4), 775-795. doi:10.1002/hbm.21473

Dinges, D. F., & Powell, J. W. (1985). Microcomputer analyses of performance on a portable, simple visual RT task during sustained operations. *Behav Res Meth, 17*(6), 652-655. doi:10.3758/BF03200977

Dixon, M., & Christoff, K. (2012). The decision to engage cognitive control is driven by expected reward-value: neural and behavioral evidence. *PloS one, 7*(12), e51637. doi:10.1371/journal.pone.0051637

Dixon, M., Marley, J., & Jacobs, E. A. (2003). Delay discounting by pathologicalgamblers. *J Applied Behav Anal, 36*(4), 449-458. doi:10.1901/jaba.2003.36-449

Donders, F. C. (1969). On the speed of mental processes. *Acta psychologica, 30*, 412-431. doi:10.1016/0001-6918(69)90065-1

Donner, T. H., Siegel, M., Oostenveld, R., Fries, P., Bauer, M., & Engel, A. K. (2007). Population activity in the human dorsal pathway predicts the accuracy of visual motion detection. *J Neurophysiol, 98*(1), 345-359. doi:10.1152/jn.01141.2006

Donoghue, J. P., Sanes, J. N., Hatsopoulos, N. G., & Gaal, G. (1998). Neural discharge and local field potential oscillations in primate motor cortex during voluntary movements. *J Neurophysiol, 79*(1), 159-173. doi:10.1152/jn.1998.79.1.159

Doyle, J. R., & Chen, C. H. (2010). Time is money: arithmetic discounting outperforms hyperbolic and exponential discounting. *SSRN* doi:10.2139/ssrn.1609594

Doyle, J. R., & Chen, C. H. (2012). The wages of waiting and simple models of delay discounting. *SSRN*. doi:10.2139/ssrn.2008283

Doyle, J. R., Yarrow, K., & Brown, P. (2005). Lateralization of event-related beta desynchronization in the eeg during pre-cued reaction time tasks. *Clin Neurophysiol, 116*(8), 1879-1888. doi:10.1016/j.clinph.2005.03.017

Drake, A. R., & Kohlmeyer, J. M. (2010). Risk-taking in new project selection: additive effects of bonus incentives and past performance history. *Adv Account, 26*(2), 207-220. doi:10.1016/j.adiac.2010.04.005

Dreisbach, G., & Fischer, R. (2012). Conflicts as aversive signals. *Brain Cogn, 78*(2), 94-98. doi:10.1016/j.bandc.2011.12.003

Duckworth, K. L., Bargh, J. A., Garcia, M., & Chaiken, S. (2002). The automatic evaluation of novel stimuli. *Psychol Sci, 13*(6), 513-519. doi:10.1111/1467-9280.00490

Duque, J., Greenhouse, I., Labruna, L., & Ivry, R. B. (2017). Physiological markers of motor inhibition during human behavior. *Trends Neurosci, 40*(4), 219-236. doi:10.1016/j.tins.2017.02.006

Durstewitz, D., & Seamans, J. K. (2008). The dual-state theory of prefrontal cortex dopamine function with relevance to catechol-o-methyltransferase genotypes and schizophrenia. *Biol Psychiatr, 64*(9), 739-749. doi:10.1016/j.biopsych.2008.05.015

Durstewitz, D., Seamans, J. K., & Sejnowski, T. J. (2000). Dopamine-mediated stabilization of delay-period activity in a network model of prefrontal cortex. *J Neurophysiol, 83*(3), 1733-1750. doi:10.1152/jn.2000.83.3.1733

Eagle, D. M., Bari, A., & Robbins, T. W. (2008). The neuropsychopharmacology of action inhibition: cross-species translation of the stop-signal and Go/No-Go tasks. *Psychopharmacol, 199*(3), 439-456. doi:10.1007/s00213-008-1127-6

Eagle, D. M., & Robbins, T. W. (2003). Inhibitory control in rats performing a stop-signal reaction-time task: effects of lesions of the medial striatum and d-amphetamine. *Behav Neurosci, 117*(6), 1302-1317. doi:10.1037/0735-7044.117.6.1302

Earle, F. (2004). *The construct of psychological fatigue: A psychometric and experimental analysis*. University of Hull, Hull, United Kingdom.

Easterbrook, J. A. (1959). The effect of emotion oon cue utilization and the organization of behavior. *Psychol Rev, 66*(3), 183-201. doi:10.1037/h0047707

Ebersole, J. S., & Ebersole, S. M. (2010). Combining MEG and EEG source modeling in epilepsy evaluations. *J Clin Neurophysiol, 27*(6), 360-371. doi:10.1097/WNP.0b013e318201ffc4

Eckhorn, R., Bauer, R., Jordan, W., Brosch, M., Kruse, W., Munk, M., & Reitboeck, H. J. (1988). Coherent oscillations: a mechanism of feature linking in the visual cortex? Multiple electrode and correlation analyses in the cat. *Biol Cybern, 60*(2), 121-130. doi:10.1007/bf00202899

Efklides, A., Kourkoulou, A., Mitsiou, F., & Ziliaskopoulou, D. (2006). Metacognitive knowledge of effort, personality factors, and mood state: their relationships with effort-related metacognitive experiences. *Metacogn Learning*, 1(1), 33-49.

Eisenberger, R. (1992). Learned industriousness. *Psychol Rev*, 99(2), 248-267. doi:10.1037/0033-295x.99.2.248

Elliot, A. J. (2006). The hierarchical model of approach-avoidance motivation. *Motiv Emot*, 30(2), 111-116. doi: 10.1007/s11031-006-9028-7

Elliott, R. (1969). Tonic heart rate: experiments on the effects of collative variables lead to a hypothesis about its motivational significance. *J Pers Soc Psychol*, 12(3), 211-228.

Elpidorou, A. (2018). The good of boredom. *Philos Psychol, 31*(3), 323-351. doi:10.1080/09515089.2017.1346240

Engel, A. K., & Fries, P. (2010). Beta-band oscillations. signalling the status quo? *Curr Opin Neurobiol, 20*(2), 156-165. doi:10.1016/j.conb.2010.02.015

Engelmann, J. B., Damaraju, E., Padmala, S., & Pessoa, L. (2009). Combined effects of attention and motivation on visual task performance: transient and sustained motivational effects. *Front Human Neurosci, 3*, 4. doi:10.3389/neuro.09.004.2009

Engelmann, J. B., & Pessoa, L. (2007). Motivation sharpens exogenous spatial attention. *Emot, 7*(3), 668-674. doi:10.1037/1528-3542.7.3.668

Erbil, N., & Ungan, P. (2007). Changes in the alpha and beta amplitudes of the central eeg during the onset, continuation, and offset of long-duration repetitive hand movements. *Brain Res, 1169*, 44-56. doi:10.1016/j.brainres.2007.07.014

Ergenoglu, T., Demiralp, T., Bayraktaroglu, Z., Ergen, M., Beydagi, H., & Uresin, Y. (2004). Alpha rhythm of the EEG modulates visual detection performance in humans. *Brain Res Cogn Brain Res, 20*(3), 376-383. doi:10.1016/j.cogbrainres.2004.03.009

Ert, E., & Erev, I. (2013). On the descriptive value of loss aversion in decisions under risk: six clarifications. *Judgm Decis Mak, 8*(3), 214-235. doi:10.2139/ssrn.1012022

Espenhahn, S., de Berker, A. O., van Wijk, B. C. M., Rossiter, H. E., & Ward, N. S. (2017). Movement-related beta oscillations show high intra-individual reliability. *Neuroimage, 147*, 175-185. doi:10.1016/j.neuroimage.2016.12.025

Estle, S. J., Green, L., Myerson, J., & Holt, D. D. (2007). Discounting of monetary and directly consumable rewards. *Psychol Sci, 18*(1), 58-63. doi:10.1111/j.1467-9280.2007.01849.x

Evans, J. S. (2008). Dual-processing accounts of reasoning, judgment, and social cognition. *Annu Rev Psychol, 59*, 255-278. doi:10.1146/annurev.psych.59.103006.093629

Everitt, B. J., Cardinal, R. N., Parkinson, J. A., & Robbins, T. W. (2003). Appetitive behavior: impact of amygdala-dependent mechanisms of emotional learning. *Ann N Y Acad Sci*, 985, 233-250.

Fairclough, S. H., & Houston, K. (2004). A metabolic measure of mental effort. *Biol Psychol, 66*(2), 177-190. doi:10.1016/j.biopsycho.2003.10.001

Fairclough, S. H., & Roberts, J. S. (2011). Effects of performance feedback on cardiovascular reactivity and frontal EEG asymmetry. *Int J Psychophysiol, 81*(3), 291-298. doi:10.1016/j.ijpsycho.2011.07.012

Fallgatter, A. J., & Strik, W. K. (1997). Right frontal activation during the continuous performance test assessed with near-infrared spectroscopy in healthy subjects. *Neurosci Lett*, 223(2), 89-92. doi:10.1016/s0304-3940(97)13416-4

Fanselow, M. S. (1994). Neural organization of the defensive behavior system responsible for fear. *Psychon Bull Rev, 1*(4), 429-438. doi:10.3758/bf03210947

Faust, T. W., Assous, M., Tepper, J. M., & Koós, T. (2016). Neostriatal GABAergic interneurons mediate cholinergic inhibition of spiny projection neurons. *J Neurosci, 36*(36), 9505-9511.

Feige, B., Aertsen, A., & Kristeva-Feige, R. (2000). Dynamic synchronization between multiple cortical motor areas and muscle activity in phasic voluntary movements. *J Neurophysiol, 84*(5), 2622-2629. doi:10.1152/jn.2000.84.5.2622

Feng, S. F., Schwemmer, M., Gershman, S. J., & Cohen, J. D. (2014). Multitasking versus multiplexing: Toward a normative account of limitations in the simultaneous execution of control-demanding behaviors. *Cogn Affect Behav Neurosci, 14*(1), 129-146. doi:10.3758/s13415-013-0236-9

Fervaha, G., Foussias, G., Agid, O., & Remington, G. (2013). Neural substrates underlying effort computation in schizophrenia. *Neurosci Biobehav Rev, 37*(10 Pt 2), 2649-2665. doi:10.1016/j.neubiorev.2013.09.001

Festinger, L. (1942). A theoretical interpretation of shifts in level of aspiration. *Psychol Rev*, 49(3), 235. doi:10.1037/h0055434

Feshchenko, V. A., Veselis, R. A., & Reinsel, R. A. (1997). Comparison of the EEG effects of midazolam, thiopental, and propofol: the role of underlying oscillatory systems. *Neuropsychobiol, 35*(4), 211-220. doi:10.1159/000119347

Filipovic, S. R., Jahanshahi, M., & Rothwell, J. C. (2000). Cortical potentials related to the Nogo decision. *Exp Brain Res, 132*(3), 411-415. doi:10.1007/s002210000349

Filipović, S. R., Jahanshahi, M., & Rothwell, J. C. (2001). Uncoupling of contingent negative variation and alpha band event-related desynchronization in a Go/No-Go task. *Clin Neurophysiol,* 112(7), 1307-1315. doi:10.1016/s1388-2457(01)00558-2

Fingelkurts, A. A., Fingelkurts, A. A., Kivisaari, R., Pekkonen, E., Ilmoniemi, R. J., & Kähkönen, S. (2004). The interplay of lorazepam-induced brain oscillations: microstructural electromagnetic study. *Clin Neurophysiol, 115*(3), 674-690. doi:10.1016/j.clinph.2003.10.025

Fink, M., Weinfeld, R. E., Schwartz, M. A., & Conney, A. H. (1976). Blood levels and electroencephalographic effects of siazepam and bromazepam. *Clin Pharmacol Ther, 20*(2), 184-191. doi:10.1002/cpt1976202184

Fischer, P., Pogosyan, A., Herz, D. M., Cheeran, B., Green, A. L., Fitzgerald, J., . . . Foltynie, T. (2017). Subthalamic nucleus gamma activity increases not only during movement but also during movement inhibition. *Elife, 6*, e23947.

Floresco, S. B. (2013). Prefrontal dopamine and behavioral flexibility: shifting from an "inverted-u" toward a family of functions. *Front Neurosci, 7*, 62. doi:10.3389/fnins.2013.00062

Fonken, Y. M., Rieger, J. W., Tzvi, E., Crone, N. E., Chang, E., Parvizi, J., . . . Kramer, U. M. (2016). Frontal and motor cortex contributions to response inhibition: evidence from electrocorticography. *J Neurophysiol, 115*(4), 2224-2236. doi:10.1152/jn.00708.2015

Formaggio, E., Storti, S. F., Avesani, M., Cerini, R., Milanese, F., Gasparini, A., . . . Manganotti, P. (2008). EEG and FMRI coregistration to investigate the cortical oscillatory activities during finger movement. *Brain Topogr, 21*(2), 100-111. doi:10.1007/s10548-008-0058-1

Fontanesi, L., Palminteri, S., & Lebreton, M. (2019). Decomposing the effects of context valence and feedback information on speed and accuracy during reinforcement learning: a meta-analytical approach using diffusion decision modeling. *Cogn Affect Behav Neurosci*, 19(3), 490-502. doi:10.3758/s13415-019-00723-1

Fox, A. S., Bakermans-Kranenburg, M. J., Yoo, K. H., Bowman, L. C., Cannon, E. N., Vanderwert, R. E., . . . van IJzendoorn, M. H. (2016). Assessing human mirror activity with eeg mu rhythm: a meta-analysis. *Psychol Bull, 142*(3), 291. doi:10.1037/bul0000031

Foxe, J. J., & Snyder, A. C. (2011). The role of alpha-band brain oscillations as a sensory suppression mechanism during selective attention. *Front Psychol, 2*, 154. doi:10.3389/fpsyg.2011.00154

Frank, M. J., & O'Reilly, R. C. (2006). A mechanistic account of striatal dopamine function in human cognition: psychopharmacological studies with cabergoline and haloperidol. *Behav Neurosci, 120*(3), 497-517. doi:10.1037/0735-7044.120.3.497

Frank, M. J., Woroch, B. S., & Curran, T. (2005). Error-related negativity predicts reinforcement learning and conflict biases. *Neuron, 47*(4), 495-501. doi:10.1016/j.neuron.2005.06.020

Frankenhauser, M. (1986). A psychobiological framework for research on human stress and coping. *Physiol Soc Perspec*, 101-116.

Franzen, P. L., Gianaros, P. J., Marsland, A. L., Hall, M. H., Siegle, G. J., Dahl, R. E., & Buysse, D. J. (2011). Cardiovascular reactivity to acute psychological stress following sleep deprivation. *Psychosomatic Med, 73*(8), 679. doi:10.1097/PSY.0b013e31822ff440

Fredrickson, B. L., Mancuso, R. A., Branigan, C., & Tugade, M. M. (2000). The undoing effect of positive emotions. *Motiv Emot, 24*(4), 237-258. doi:10.1023/A:1010796329158

Freeman, S. M., Razhas, I., & Aron, A. R. (2014). Top-down response suppression mitigates action tendencies triggered by a motivating stimulus. *Curr Biol*, 24(2), 212-216. doi:10.1016/j.cub.2013.12.019

Frey, J. N., Mainy, N., Lachaux, J. P., Muller, N., Bertrand, O., & Weisz, N. (2014). Selective modulation of auditory cortical alpha activity in an audiovisual spatial attention task. *J Neurosci, 34*(19), 6634-6639. doi:10.1523/jneurosci.4813-13.2014

Freydefont, L., Gendolla, G. H., & Silvestrini, N. (2012). Beyond valence: the differential effect of masked anger and sadness stimuli on effort-related cardiac response. *Psychophysiol*, 49(5), 665-671. doi:10.1111/j.1469-8986.2011.01340.x

Friedman, N. P., & Miyake, A. (2004). The relations among inhibition and interference control functions: a latent-variable analysis. *J Exp Psychol Gen, 133*(1), 101-135. doi:10.1037/0096-3445.133.1.101

Fries, P., Reynolds, J. H., Rorie, A. E., & Desimone, R. (2001). Modulation of oscillatory neuronal synchronization by selective visual attention. *Sci, 291*(5508), 1560-1563. doi:10.1126/science.1055465

Frith, C. (2002). Attention to action and awareness of other minds. *Conscious Cogn, 11*(4), 481-487. doi:10.1016/S1053-8100(02)00022-3

Fry, A., Mullinger, K. J., O'Neill, G. C., Barratt, E. L., Morris, P. G., Bauer, M., . . . Brookes, M. J. (2016). Modulation of post-movement beta rebound by contraction force and rate of force development. *Hum Brain Mapp, 37*(7), 2493-2511. doi:10.1002/hbm.23189

Fry, A., Mullinger, K. J., O'neill, G. C., Barratt, E. L., Morris, P. G., Bauer, M., . . . Brookes, M. J. (2016). Modulation of post-movement beta rebound by contraction force and rate of force development. *Hum Brain Mapping, 37*(7), 2493-2511. doi:10.1002/hbm.23189

Fry, A., Mullinger, K. J., O'Neill, G. C., Brookes, M. J., & Folland, J. P. (2017). The effect of physical fatigue on oscillatory dynamics of the sensorimotor cortex. *Acta Physiol, 220*(3), 370-381. doi:10.1111/apha.12843

Fu, K. M., Foxe, J. J., Murray, M. M., Higgins, B. A., Javitt, D. C., & Schroeder, C. E. (2001). Attention-dependent suppression of distracter visual input can be cross-modally cued asindexed by anticipatory parieto-occipital alpha-band oscillations. *Brain Res Cogn Brain Res, 12*(1), 145-152. doi:10.1016/S0926-6410(01)00034-9

Fujita, K., Gollwitzer, P. M., & Oettingen, G. (2007). Mindsets and pre-conscious open-mindedness to incidental information. *J Exp Soc Psychol*, 43(1), 48-61. doi:10.1016/j.jesp.2005.12.004

Fujiyama, H., Hinder, M. R., Schmidt, M. W., Garry, M. I., & Summers, J. J. (2012). Age-related differences in corticospinal excitability and inhibition during coordination of upper and lower limbs. *Neurobiol Aging*, *33*(7), 1484.e1481-1414. doi:10.1016/j.neurobiolaging.2011.12.019

Fujiyama, H., Hinder, M. R., & Summers, J. J. (2013). Functional role of left pmd and left M1 during preparation and execution of left hand movements in older adults. *J Neurophysiol, 110*(5), 1062-1069. doi:10.1152/jn.00075.2013

Funderud, I., Lindgren, M., Løvstad, M., Endestad, T., Voytek, B., Knight, R. T., & Solbakk, A. K. (2012). Differential Go/NoGo activity in both contingent negative variation and spectral power. *PloS one,* 7(10), e48504. doi:10.1371/journal.pone.0048504

Fuster, J. (2015). *The prefrontal cortex*: Academic Press.

Gabor, D. (1946). Theory of communication. part 1: the analysis of information. *J Electr Eng,* 93(26), 429-441. doi:10.1049/ji-3-2.1946.0074

Gaetz, W., & Cheyne, D. (2006). Localization of sensorimotor cortical rhythms induced bytactile stimulation using spatially filtered MEG. *Neuroimage, 30*(3), 899-908. doi:10.1016/j.neuroimage.2005.10.009

Gaetz, W., Edgar, J. C., Wang, D. J., & Roberts, T. P. (2011). Relating MEG measured motor cortical oscillations to resting gamma-aminobutyric acid (GABA) Concentration. *Neuroimage, 55*(2), 616-621. doi:10.1016/j.neuroimage.2010.12.077

Gailliot, M. T., & Baumeister, R. F. (2007). The physiology of willpower: linking blood glucose to self-control. *Pers Soc Psychol Rev, 11*(4), 303-327. doi:10.1177/1088868307303030

Gal, D., & Rucker, D. D. (2018). The loss of loss aversion: will it loom larger than its gain? *J Consum Psychol, 28*(3), 497-516. doi:10.1002/jcpy.1047

Galan, L., Biscay, R., Rodriguez, J. L., Perez-Abalo, M. C., & Rodriguez, R. (1997). Testing topographic differences between event related brain potentials by

using non-parametric combinations of permutation tests. *Electroencephalogr Clin Neurophysiol, 102*(3), 240-247. doi:10.1016/s0013-4694(96)95155-3

Garavan, H., Ross, T., & Stein, E. (1999). Right hemispheric dominance of inhibitory control: an event-related functional MRI study. *Nat Acad Sci, 96*(14), 8301-8306. doi:10.1073/pnas.96.14.8301

Garavan, H., Ross, T. J., Murphy, K., Roche, R. A., & Stein, E. A. (2002). Dissociable executive functions in the dynamic control of behavior: inhibition, error detection, and correction. *Neuroimage, 17*(4), 1820-1829.

Gastaut, H. J. (1952). Etude electrocorticographique de la réactivité des rythmes rolandiques. *Rev Neurol (Paris), 87*, 176-182.

Gehring, W. J., & Willoughby, A. R. (2002). The medial frontal cortex and the rapid processing of monetary gains and losses. *Sci, 295*(5563), 2279-2282. doi:10.1126/science.1066893

Gendolla, G. H. (2012). Implicit affect primes effort: a theory and research on cardiovascular response. *Int J Psychophysiol*, 86(2), 123-135. doi:10.1016/j.ijpsycho.2012.05.003

Gendolla, G. H., Brinkmann, K., & Silvestrini, N. (2012). Gloomy and lazy? On the impact of mood and depressive symptoms on effort-related cardiovascular response. *American Psychol Association*. doi:10.1037/13090-007

Gendolla, G. H., & Krüsken, J. (2002). Informational mood impact on effort-related cardiovascular response: the diagnostic value of mood counts. *Emotion*, 2(3), 251-262. doi:10.1037/1528-3542.2.3.251

Gendolla, G. H., & Richter, M. (2006). Ego-involvement and the difficulty law of motivation: effects on performance-related cardiovascular response. *Pers Soc Psychol Bull*, 32(9), 1188-1203. doi:10.1177/0146167206288945

Gendolla, G. H., Wright, R. A., & Richter, M. (2012). Effort intensity: some insights from the cardiovascular dystem. *Handbook Hum Motiv*, 420-438.

Gevins, A., Smith, M. E., McEvoy, L., & Yu, D. (1997). High-resolution EEG mapping of cortical activation related to working memory: effects of task difficulty, type of processing, and practice. *Cerebral cortex (New York, NY: 1991), 7*(4), 374-385.

Gevins, A., Smith, M. E., McEvoy, L., & Yu, D. (1997). High-resolution EEG mapping of cortical activation related to working memory: effects of task difficulty, type of processing, and practice. Cereb Cortex, 7(4), 374-385. doi:10.1093/cercor/7.4.374

Gianotti, L. R., Figner, B., Ebstein, R. P., & Knoch, D. (2012). Why some people discount more than others: baseline activation in the dorsal PFC mediates the link between comt genotype and impatient choice. *Front Neurosci, 6*, 54. doi:10.3389/fnins.2012.00054

Gibson, E. L. (2007). Carbohydrates and mental function: feeding or impeding the brain? *Nutr Bull, 32*(s1), 71-83. doi:10.1111/j.1467-3010.2007.00606.x

Gilbertson, T., Lalo, E., Doyle, L., Di Lazzaro, V., Cioni, B., & Brown, P. (2005). Existing motor state is favored at the expense of new novement during 13-35 hz oscillatory synchrony in the human corticospinal system. *J Neurosci, 25*(34), 7771-7779. doi:10.1523/jneurosci.1762-05.2005

Gips, B., van der Eerden, J. P., & Jensen, O. (2016). A biologically plausible mechanism for neuronal coding organized by the phase of alpha oscillations. *Eur J Neurosci, 44*(4), 2147-2161. doi:10.1111/ejn.13318

Glimcher, P. W. (2004). *Decisions, uncertainty, and the brain: the science of neuroeconomics*. Cambridge, Massachusetts: MIT press.

Glimcher, P. W., & Fehr, E. (2014). *Neuroeconomics: Decision making and the brain.* San Diego, CA: Academic Press.

Gold, J. M., Strauss, G. P., Waltz, J. A., Robinson, B. M., Brown, J. K., & Frank, M. J. (2013). Negative symptoms of schizophrenia are associated with abnormal effort-cost computations. *Biol Psychiatry, 74*(2), 130-136. doi:10.1016/j.biopsych.2012.12.022

Gold, J. M., Waltz, J. A., & Frank, M. J. (2015). Effort cost computation in schizophrenia: a commentary on the recent literature. *Biol Psychiatry, 78*(11), 747-753. doi:10.1016/j.biopsych.2015.05.005

Gollwitzer, P. M. (1990). Action phases and mind-sets. *Handbook of motivation and cognition: Foundations of social behavior*, 2, 53-92. doi:10.1.1.335.3962

Gollwitzer, P. M. (1999). Implementation intentions: strong effects of simple plans. *American psychologist*, 54(7), 493. doi: 10.1037/0003-066X.54.7.493

Gollwitzer, P. M., & Bargh, J. A. (1996). The psychology of action: *Linking cognition and motivation to behavior*. New York, United States: Guilford

Gollwitzer, P. M. (2012). Mindset theory of action phases. Press.

Gollwitzer, P. M., & Keller, L. (2016). Mindset theory. *Encyclopedia of personal and individual differences*, 1-8. doi:10.1007/978-3-319-28099-8_1141-1

Golombok, S., & Lader, M. (1984). The psychopharmacological effects of premazepam, diazepam and placebo in healthy human Subjects. *Clin Pharmacol, 18*(2), 127-133. doi:10.1111/j.1365-2125.1984.tb02444.x

Gomez-Ramirez, M., Kelly, S. P., Molholm, S., Sehatpour, P., Schwartz, T. H., & Foxe, J. J. (2011). Oscillatory sensory selection mechanisms during intersensory attention to rhythmic auditory and visual inputs: a human

electrocorticographic investigation. *J Neurosci, 31*(50), 18556-18567. doi:10.1523/jneurosci.2164-11.2011

Gose, K., & Sadrieh, A. (2012). Fair wages when employers face the risk of losing money. *Econ Lett, 117*(3), 687-690. doi:10.1016/j.econlet.2011.12.073

Grafman, J. (1994). Alternative frameworks for the conceptualization of prefrontal lobe functions. *Handbook Neuropsychol, 9*(7), 187-199.

Graham, F. K. (1979). Distinguishing among orienting, fefense, and startle reflexes. *Orienting Reflex Hum*.

Green, L., & Arduini, A. A. (1954). Hippocampal electrical activity in arousal. *J Neurophysiol, 17*(6), 533-557. doi:10.1152/jn.1954.17.6.533

Green, L., Fry, A. F., & Myerson, J. (1994). Discounting of delayed rewards: a life-span comparison. *Psychol Sci, 5*(1), 33-36. doi:10.1111/j.1467-9280.1994.tb00610.x

Green, L., & Myerson, J. (2004). A discounting framework for choice with delayed and probabilistic rewards. *Psychol Bull, 130*(5), 769-792. doi:10.1037/0033-2909.130.5.769

Green, L., & Myerson, J. (2013). How many impulsivities? A discounting perspective. *J Exp Anal Behav, 99*(1), 3-13. doi:10.1002/jeab.1

Green, L., Myerson, J., Oliveira, L., & Chang, S. E. (2013). Delay discounting of monetary rewards over a wide range of amounts. *J Exp Anal Behav, 100*(3), 269-281. doi:10.1002/jeab.45

Green, L., Myerson, J., & Ostaszewski, P. (1999). Amount of reward has opposite effects on the discounting of delayed and probabilistic outcomes. J Exp Psychol Learn Mem Cogn, 25(2), 418-427. doi:10.1037//0278-7393.25.2.418

Greenwald, M. K., Cook, E. W., & Lang, P. J. (1989). Affective judgment and psychophysiological response: dimensional covariation in the evaluation of pictorial stimuli. *J Psychophysiol*.

Groppe, D. M., Urbach, T. P., & Kutas, M. (2011). Mass univariate analysis of event-related brain potentials/fields I: a critical tutorial review. *Psychophysiol*, 48(12), 1711-1725. doi:10.1111/j.1469-8986.2011.01273.x

Grosbras, M. H., & Paus, T. (2002). Transcranial magnetic stimulation of the human frontal eye field: effects on visual perception and attention. *J Cogn Neurosci, 14*(7), 1109-1120. doi:10.1162/089892902320474553

Grosbras, M. H., & Paus, T. (2003). Transcranial magneticstimulation of the human frontal eye field facilitates visual awareness. *Eur J Neurosci, 18*(11), 3121-3126. doi:10.1111/j.1460-9568.2003.03055.x

Guitart-Masip, M., Chowdhury, R., Sharot, T., Dayan, P., Duzel, E., & Dolan, R. J. (2012). Action controls dopaminergic enhancement of reward representations. *Proc Nat Acad Sci, 109*(19), 7511-7516. doi:10.1073/pnas.1202229109

Guitart-Masip, M., Economides, M., Huys, Q. J., Frank, M. J., Chowdhury, R., Duzel, E., . . . Dolan, R. J. (2014). Differential, but not opponent, effects of L -Dopa and citalopram on action learning with reward and punishment. *Psychopharmacol, 231*(5), 955-966. doi:10.1007/s00213-013-3313-4

Guitart-Masip, M., Fuentemilla, L., Bach, D. R., Huys, Q. J., Dayan, P., Dolan, R. J., & Duzel, E. (2011). Action dominates valence in anticipatory representations in the human striatum and dopaminergic midbrain. *J Neurosci*, 31(21), 7867-7875. doi:10.1523/jneurosci.6376-10.2011

Guitart-Masip, M., Huys, Q. J., Fuentemilla, L., Dayan, P., Duzel, E., & Dolan, R. J. (2012). Go and No-Go learning in reward and punishment: interactions between affect and effect. *Neuroimage, 62*(1), 154-166. doi:10.1016/j.neuroimage.2012.04.024

Guo, J. (2012). Optimal sample size planning for the Wilcoxon–Mann–Whitney and van Elteren tests under cost constraints. *J App Stat,* 39(10), 2153-2164. doi:10.1080/02664763.2012.702265

Guthrie, D., & Buchwald, J. S. (1991). Significance testing of difference potentials. *Psychophysiol, 28*(2), 240-244. doi:10.1111/j.1469-8986.1991.tb00417.x

Haber, S. N., & Knutson, B. (2010). The reward circuit: linking primate anatomy and human imaging. *Neuropsychopharmacol, 35*(1), 4. doi:10.1038/npp.2009.129

Haegens, S., Händel, B. F., & Jensen, O. (2011). Top-down controlled alpha band activity in somatosensory areas determines behavioral performance in a discrimination task. *J Neurosci, 31*(14), 5197-5204. doi:10.1523/JNEUROSCI.5199-10.2011

Haegens, S., Nácher, V., Luna, R., Romo, R., & Jensen, O. (2011). α-Oscillations in the monkey sensorimotor network influence discrimination performance by rhythmical inhibition of neuronal spiking. *Proc Natl Acad Sci, 108*(48), 19377-19382. doi:10.1073/pnas.1117190108

Hagger, M. S., Wood, C., Stiff, C., & Chatzisarantis, N. L. (2010). Ego depletion and the strength model of self-control: a meta-analysis. *Psychol Bull, 136*(4), 495-525. doi:10.1037/a0019486

Hall, S. D., Barnes, G. R., Furlong, P. L., Seri, S., & Hillebrand, A. (2010). Neuronal network pharmacodynamics of GABAergic modulation in the human cortex

determined using pharmaco-magnetoencephalography. *Hum Brain Mapp, 31*(4), 581-594. doi:10.1002/hbm.20889

Hall, S. D., Stanford, I. M., Yamawaki, N., McAllister, C. J., Ronnqvist, K. C., Woodhall, G. L., & Furlong, P. L. (2011). The role of GABAergic modulation in motor function related neuronal network activity. *Neuroimage, 56*(3), 1506-1510. doi:10.1016/j.neuroimage.2011.02.025

Hämäläinen, M., Hari, R., Ilmoniemi, R. J., Knuutila, J., & Lounasmaa, O. V. (1993). Magnetoencephalography—theory, instrumentation, and applications to noninvasive studies of the working human brain. *Rev Modern Phys, 65*(2), 413. doi:10.1103/RevModPhys.65.413

Hammar, A., & Ardal, G. (2009). Cognitive functioning in major depression--a summary. *Front Hum Neurosci, 3*, 26. doi:10.3389/neuro.09.026.2009

Handel, B. F., Haarmeier, T., & Jensen, O. (2011). Alpha oscillations correlate with the successful inhibition of unattended stimuli. *J Cogn Neurosci, 23*(9), 2494-2502. doi:10.1162/jocn.2010.21557

Hannan, R. L., Hoffman, V. B., & Moser, D. V. (2005). Bonus versus penalty: does contract frame affect employee effort? In *Exp Bus Res* (pp. 151-169): Springer.

Hanslmayr, S., Klimesch, W., Sauseng, P., Gruber, W., Doppelmayr, M., Freunberger, R., & Pecherstorfer, T. (2005). Visual discrimination performance is related to decreased alpha amplitude but increased phase locking. *Neurosci Lett, 375*(1), 64-68. doi:10.1016/j.neulet.2004.10.092

Hanslmayr, S., Pastotter, B., Bauml, K. H., Gruber, S., Wimber, M., & Klimesch, W. (2008). The electrophysiological dynamics of interference during the stroop task. *J Cogn Neurosci, 20*(2), 215-225. doi:10.1162/jocn.2008.20020

Hanslmayr, S., Gross, J., Klimesch, W., & Shapiro, K. L. (2011). The role of α oscillations in temporal attention. *Brain Res Rev*, 67(1-2), 331-343. doi:10.1016/j.brainresrev.2011.04.002

Hari, R., Parkkonen, L., & Nangini, C. (2010). The brain in time: insights from neuromagnetic recordings. *Ann N Y Acad Sci, 1191*, 89-109. doi:10.1111/j.1749-6632.2010.05438.x

Harkins, S. G. (2006). Mere effort as the mediator of the evaluation-performance relationship. *J Pers Soc Psychol*, 91(3), 436-455. doi:10.1037/0022-3514.91.3.436

Harmony, T., Alba, A., Marroquín, J. L., & González-Frankenberger, B. (2009). Time-frequency-topographic analysis of induced power and synchrony of EEG signals during a Go/No-Go task. *Int J Psychophysiol*, 71(1), 9-16. doi:10.1016/j.ijpsycho.2008.07.020

Harnishfeger, K. K. (1995). The development of cognitive inhibition: theories, definitions, and research evidence. In *Interference and inhibition in cognition* (pp. 175-204). Amsterdam, Netherlands: Elsevier.

Hartlage, S., Alloy, L. B., Vázquez, C., & Dykman, B. (1993). Automatic and effortful processing in depression. *Psychol Bull, 113*(2), 247. doi:10.1037/0033-2909.113.2.247

Hartman, M. N., & Slapničar, S. (2015). An experimental study of the effects of negative, capped and deferred bonuses on risk taking in a multi-period setting. *J Manag Govern, 19*(4), 875-896. doi:10.1007/s10997-014-9297-6

Hartmann, M. N., Hager, O. M., Tobler, P. N., & Kaiser, S. (2013). Parabolic discounting of monetary rewards by physical effort. *Behav Processes, 100*, 192-196. doi:10.1016/j.beproc.2013.09.014

Hasher, L. (1979). Automatic and effortful processes in memory. *J Exp Psychol, 108*(3), 356. doi:10.1037/0096-3445.108.3.356

Hasher, L., & Zacks, R. T. (1988). Working memory, comprehension, and aging: a review and a new view. In *Psychol Learning Mot* (Vol. 22, pp. 193-225). Amsterdam, Netherlands: Elsevier.

Hayasaka, S., & Nichols, T. E. (2003). Validating cluster size inference: random field and permutation methods. *Neuroimage, 20*(4), 2343-2356. doi:10.1016/j.neuroimage.2003.08.003

Hayasaka, S., & Nichols, T. E. (2004). Combining voxel iintensity and cluster extent with permutation test framework. *Neuroimage, 23*(1), 54-63. doi:10.1016/j.neuroimage.2004.04.035

Hazy, T. E., Frank, M. J., & O'Reilly, R. C. (2006). Banishing the homunculus: making working memory work. *Neurosci, 139*(1), 105-118. doi:10.1016/j.neuroscience.2005.04.067

Heckhausen, H. (1987). Wünschen—Wählen—Wollen. In Jenseits des Rubikon (pp. 3-9): Springer.

Heckhausen, H., & Gollwitzer, P. M. (1987). Thought contents and cognitive functioning in motivational versus volitional states of mind. *Mot Emot,* 11(2), 101-120. doi:10.1007/BF00992338

Heidig, W., Wentzel, D., Tomczak, T., Wiecek, A., & Faltl, M. (2017). “Supersize me!” The effects of cognitive effort and goal frame on the persuasiveness of upsell offers. *J Serv Manag, 28*(3), 541-562.

Heinrichs-Graham, E., McDermott, T. J., Mills, M. S., Coolidge, N. M., & Wilson, T. W. (2017). Transcranial direct-current stimulation modulates offline visual

oscillatory activity: a magnetoencephalography study. *Cortex, 88*, 19-31. doi:10.1016/j.cortex.2016.11.016

Heinrichs-Graham, E., McDermott, T. J., Mills, M. S., Wiesman, A. I., Wang, Y. P., Stephen, J. M., . . . Wilson, T. W. (2018). The lifespan trajectory of neural oscillatory activity in the motor system. *Dev Cogn Neurosci*, 30, 159-168. doi:10.1016/j.dcn.2018.02.013

Henry, M. J., & Obleser, J. (2012). Frequency modulation entrains slow neural oscillations and optimizes human listening behavior. *Proc Natl Acad Sci 109*(49), 20095-20100. doi:10.1073/pnas.1213390109

Henson, R. N., Mouchlianitis, E., & Friston, K. J. (2009). MEG and EEG data fusion: simultaneous localisation of face-evoked responses. *Neuroimage, 47*(2), 581-589. doi:10.1016/j.neuroimage.2009.04.063

Herrmann, C. S., Grigutsch, M., & Busch, N. A. (2005). EEG oscillations and wavelet analysis. *Event-Relat Potential Methods Handb*, 229.

Herreras, O. (2016). Local field potentials: myths and misunderstandings. *Front Neural Circuits, 10*, 101. doi:10.3389/fncir.2016.00101

Herring, J. D., Thut, G., Jensen, O., & Bergmann, T. O. (2015). Attention modulates tms-locked alpha oscillations in the visual cortex. *J Neurosci, 35*(43), 14435-14447. doi:10.1523/jneurosci.1833-15.2015

Hervey, A. S., Epstein, J. N., Curry, J. F., Tonev, S., Eugene Arnold, L., Keith Conners, C., . . . Hechtman, L. (2006). Reaction time distribution analysis of neuropsychological performance in an ADHD sample. *Child Neuropsychol, 12*(2), 125-140. doi:10.1080/09297040500499081

Hess, T. M., & Ennis, G. E. (2012). Age differences in the effort and costs associated with cognitive activity. *J Gerontol B Psychol Sci Soc Sci, 67*(4), 447-455. doi:10.1093/geronb/gbr129

Hilgetag, C. C., Théoret, H., & Pascual-Leone, A. (2001). Enhanced visual spatial attention ipsilateral to rTMS-induced 'virtual lesions' of human parietal cortex. *Nat Neurosci, 4*(9), 953-957. doi:10.1038/nn0901-953

Hillgruber, A. (1912). Fortlaufende arbeit und willensbetätigung: konigliche albertus-universitat zu konigsberg i. *Press.*

Himmelstoss, N. A., Brötzner, C. P., Zauner, A., Kerschbaum, H. H., Gruber, W., Lechinger, J., & Klimesch, W. (2015). Prestimulus amplitudes modulate p1 latencies and evoked traveling alpha waves. *Front Hum Neurosci, 9*, 302. doi:10.3389/fnhum.2015.00302

Hochman, G., Glöckner, A., & Yechiam, E. (2009). Physiological measures in identifying decision strategies. In *Foundations for Tracing Intuition* (pp. 147-167). Abingdon, UK: Psychology Press.

Hochman, G., & Yechiam, E. (2011). Loss aversion in the eye and in the heart: the autonomic nervous system's responses to losses. *J Behav Decis Mak, 24*(2), 140-156. doi:10.1002/bdm.692

Hockey, G. (2011). A motivational control theory of cognitive fatigue. *American Psychol Assoc*. doi:10.1037/12343-008

Holmes, A. P., Blair, R. C., Watson, J. D., & Ford, I. (1996). Nonparametric analysis of statistic images from functional mapping experiments. *J Cereb Blood Flow Metab, 16*(1), 7-22. doi:10.1097/00004647-199601000-00002

Holroyd, C. B., & Braver, T. S. (2016). The waste disposal problem of effortful control. *Mot Cognitive Control*, 235-260.

Holroyd, C. B., & Coles, M. G. H. (2002). The neural basis of human error processing: reinforcement learning, dopamine, and the error-related negativity. *Psychol Rev, 109*(4), 679-709. doi:10.1037/0033-295x.109.4.679

Holroyd, C. B., & Umemoto, A. (2016). The research domain criteria framework: the case for anterior cingulate cortex. *Neurosci Biobehav Rev, 71*, 418-443. doi:10.1016/j.neubiorev.2016.09.021

Holroyd, C. B., & Yeung, N. (2012). Motivation of extended behaviors by anterior cingulate cortex. *Trends Cogn Sci, 16*(2), 122-128. doi:10.1016/j.tics.2011.12.008

Holt, D. D., Green, L., & Myerson, J. (2003). Is discounting impulsive? evidence from temporal and probability discounting in gambling and non-gambling college students. *Behav Proc, 64*(3), 355-367.

Hoofs, V., Böhler, N., & Krebs, R. M. (2019). Biasing actions by incentive valence in an approach/avoidance task. *Collab Psychol*, 5(1).

Hortobagyi, T., Taylor, J. L., Petersen, N. T., Russell, G., & Gandevia, S. C. (2003). Changes in segmental and motor cortical output with contralateral muscle contractions and altered sensory inputs in humans. *J Neurophysiol, 90*(4), 2451-2459. doi:10.1152/jn.01001.2002

Hosking, J. G., Cocker, P. J., & Winstanley, C. A. (2014). Dissociable contributions of anterior cingulate cortex and basolateral amygdala on a rodent cost/benefit decision-making task of cognitive effort. *Neuropsychopharmacol, 39*(7), 1558-1567. doi:10.1038/npp.2014.27

Houtman, F., & Notebaert, W. (2013). Blinded by an error. *Cogn*, 128(2), 228-236. doi:10.1016/j.cognition.2013.04.003

Hsieh, L. T., & Ranganath, C. (2014). Frontal midline theta oscillations during working memory maintenance and episodic encoding and retrieval. Neuroimage, 85 Pt 2(0 2), 721-729. doi:10.1016/j.neuroimage.2013.08.003

Hsieh, S., & Fang, W. (2012). Elderly adults through compensatory responses can be just as capable as young adults in inhibiting the flanker influence. *Biol Psychol*, 90(2), 113-126. doi:10.1016/j.biopsycho.2012.03.006

Hsu, Y. F., Liao, K. K., Lee, P. L., Tsai, Y. A., Yeh, C. L., Lai, K. L., . . . Lee, I. H. (2011). Intermittent θ burst stimulation over primary motor cortex enhances movement-related β synchronisation. *Clin Neurophysiol*, *122*(11), 2260-2267. doi:10.1016/j.clinph.2011.03.027

Hübner, L., Godde, B., & Voelcker-Rehage, C. (2018). Older adults reveal enhanced task-related beta power decreases during a force modulation task. *Behav Brain Res*, 345, 104-113. doi:10.1016/j.bbr.2018.02.028

Hügelschäfer, S., & Achtziger, A. (2014). On confident men and rational women: It's all on your mind (set). *J Econ Psychol*, 41, 31-44. doi:10.1016/j.joep.2013.04.001

Hull, C. L. (1943). *Principles of behavior* (Vol. 422): Appleton-century-crofts New York.

Hummel, F., & Gerloff, C. (2005). Larger interregional synchrony is associated with greater behavioral success in a complex sensory integration task in humans. *Cereb Cortex*, *15*(5), 670-678. doi:10.1093/cercor/bhh170

Huster, R. J., Debener, S., Eichele, T., & Herrmann, C. S. (2012). Methods for simultaneous EEG-fMRI: an introductory review. *J Neurosci*, *32*(18), 6053-6060. doi:10.1523/jneurosci.0447-12.2012

Iani, C., Gopher, D., & Lavie, P. (2004). Effects of task difficulty and invested mental effort on peripheral vasoconstriction. *Psychophysiol, 41*(5), 789-798. doi:10.1111/j.0048-5772.2004.200.x

Ibos, G., & Freedman, D. J. (2016). Interaction between spatial and feature attention in posterior parietal cortex. *Neuron, 91*(4), 931-943.

Iijima, M., Mase, R., Osawa, M., Shimizu, S., & Uchiyama, S. (2015). Event-related synchronization and desynchronization of high-frequency electroencephalographic activity during a visual Go/No-Go paradigm. *Neuropsychobiol*, 71(1), 17-24. doi: 10.1159/000363341

Ikeda, A., & Shibasaki, H. (2003). Generator mechanisms of Bereitschaftspotentials as studied by epicortical recording in patients with intractable partial epilepsy. In *The Bereitschaftspotential* (pp. 45-59): Springer.

Ille, N., Berg, P., & Scherg, M. (2002). Artifact correction of the ongoing EEG using spatial filters based on artifact and brain signal topographies. *J Clin Neurophysiol, 19*(2), 113-124.

Inanaga, K. (1998). Frontal midline theta rhythm and mental activity. Psychiatry Clin Neurosci, 52(6), 555-566. doi:10.1046/j.1440-1819.1998.00452.x

Inzlicht, M., Schmeichel, B. J., & Macrae, C. N. (2014). Why self-control seems (but may not be) limited. *Trends Cogn Sci, 18*(3), 127-133. doi:10.1016/j.tics.2013.12.009

Ishii, A., Matsuo, T., Nakamura, C., Uji, M., Yoshikawa, T., & Watanabe, Y. (2019). Decreased alpha-band oscillatory brain activity prior to movement initiated by perception of fatigue sensation. *Sci Rep, 9*(1), 4000. doi:10.1038/s41598-019-40605-7

Ishii, R., Canuet, L., Herdman, A., Gunji, A., Iwase, M., Takahashi, H., . . . Takeda, M. (2009). Cortical oscillatory power changes during auditory oddball task revealed by spatially filtered magnetoencephalography. *Clin Neurophysiol, 120*(3), 497-504. doi:10.1016/j.clinph.2008.11.023

Ishii, R., Shinosaki, K., Ukai, S., Inouye, T., Ishihara, T., Yoshimine, T., . . . Takeda, M. (1999). Medial prefrontal cortex generates frontal midline theta rhythm. Neuroreport, 10(4), 675-679. doi:10.1097/00001756-199903170-00003

Itthipuripat, S., Wessel, J. R., & Aron, A. R. (2013). Frontal theta is a signature of successful working memory manipulation. *Exp Brain Res, 224*(2), 255-262. doi:10.1007/s00221-012-3305-3

Izhikevich, E. M., & Edelman, G. M. (2008). Large-scale model of mammalian thalamocortical systems. *Proc Natl Acad Sci, 105*(9), 3593-3598. doi:10.1073/pnas.0712231105

Jacobs, J., Hwang, G., Curran, T., & Kahana, M. J. (2006). EEG oscillations and recognition memory: theta correlates of memory retrieval and decision making. *Neuroimage, 32*(2), 978-987. doi:10.1016/j.neuroimage.2006.02.018

Jahnsen, H., & Llinás, R. (1984). Electrophysiological properties of guinea-pig thalamic neurones: an in vitro study. *J Physiol, 349,* 205-226. doi:10.1113/jphysiol.1984.sp015153

James, W. R., Reuther, J., Angus, E., Clarke, A. D., & Hunt, A. R. (2019). Inefficient eye movements: gamification improves task execution, but not fixation strategy. *Vision*, 3(3), 48. doi: 10.3390/vision3030048

Jansma, J. M., Ramsey, N. F., de Zwart, J. A., van Gelderen, P., & Duyn, J. H. (2007). fMRI study of effort and information processing in a working memory task. *Hum Brain Mapp*, 28(5), 431-440. doi:10.1002/hbm.20297

Jasper, H. H., & Penfield, W. (1949). Electrocorticograms in man: effect of voluntary movement upon the electrical activity of the precentral gyrus. *Archiv für psychiatrie und nervenkrankheiten, 183*(1-2), 163-174. doi:10.1007/BF01062488

Jauk, E., Benedek, M., & Neubauer, A. C. (2012). Tackling creativity at its roots: evidence for different patterns of EEG alpha activity related to convergent and divergent modes of task processing. *Int J Psychophysiol, 84*(2), 219-225. doi:10.1016/j.ijpsycho.2012.02.012

Jensen, O., Bonnefond, M., & VanRullen, R. (2012). An oscillatory mechanism for prioritizing salient unattended stimuli. *Trends Cogn Sci, 16*(4), 200-206. doi:10.1016/j.tics.2012.03.002

Jensen, O., Goel, P., Kopell, N., Pohja, M., Hari, R., & Ermentrout, B. (2005). On the human sensorimotor-cortex beta rhythm: sources and modeling. *Neuroimage, 26*(2), 347-355. doi:10.1016/j.neuroimage.2005.02.008

Jensen, O., & Hanslmayr, S. (2020). The role of alpha oscillations for attention and working memory. *Cognitive Neurosci*, 323.

Jensen, O., & Lisman, J. E. (2005). Hippocampal sequence-encoding driven by a cortical multi-item working memory buffer. *Trends Neurosci, 28*(2), 67-72. doi:10.1016/j.tins.2004.12.001

Jensen, J., McIntosh, A. R., Crawley, A. P., Mikulis, D. J., Remington, G., & Kapur, S. (2003). Direct activation of the ventral striatum in anticipation of aversive stimuli. *Neuron*, 40(6), 1251-1257. doi:10.1016/s0896-6273(03)00724-4

Jensen, O., & Mazaheri, A. (2010). Shaping functional architecture by oscillatory alpha activity: gating by inhibition. *Front Hum Neurosci, 4*, 186. doi:10.3389/fnhum.2010.00186

Jensen, O., & Tesche, C. D. (2002). Frontal theta activity in humans increases with memory load in a working memory task. Eur J Neurosci, 15(8), 1395-1399. doi:10.1046/j.1460-9568.2002.01975.x

Jensen, J., Smith, A. J., Willeit, M., Crawley, A. P., Mikulis, D. J., Vitcu, I., & Kapur, S. (2007). Separate brain regions code for salience vs. valence during reward prediction in humans. *Hum Brain Mapp*, 28(4), 294-302. doi:10.1002/hbm.20274

Jeneson, J. A., Westerhoff, H. V., Brown, T. R., Van Echteld, C. J., & Berger, R. (1995). Quasi-linear relationship between Gibbs free energy of ATP hydrolysis and power output in human forearm muscle. *Am J Physiol*, 268(6 Pt 1), C1474-1484. doi:10.1152/ajpcell.1995.268.6.C1474

Johnson, E. J., Häubl, G., & Keinan, A. (2007). Aspects of endowment: a query theory of value construction. *J Exp Psychol Learn Mem Cogn*, *33*(3), 461-474. doi:10.1037/0278-7393.33.3.461

Jokisch, D., & Jensen, O. (2007). Modulation of gamma and alpha activity during a working memory task engaging the dorsal or ventral stream. *J Neurosci, 27*(12), 3244-3251. doi:10.1523/jneurosci.5399-06.2007

Jones, B. A., & Rachlin, H. (2006). Social discounting. *Psychol Sci 17*(4), 283-286. doi:10.1111/j.1467-9280.2006.01699.x

Jones, B. A., & Rachlin, H. (2009). Delay, srobability, and social discounting in a public goods game. *J Exp Anal Behav, 91*(1), 61-73. doi:10.1901/jeab.2009.91-61

Jostmann, N. B., Lakens, D., & Schubert, T. W. (2009). Weight as an embodiment of importance. *Psychol Sci*, 20(9), 1169-1174. doi:10.1111/j.1467-9280.2009.02426.x

Jung, T. P., Makeig, S., Humphries, C., Lee, T. W., McKeown, M. J., Iragui, V., & Sejnowski, T. J. (2000). Removing electroencephalographic artifacts by blind source separation. *Psychophysiol, 37*(2), 163-178. doi:Removing Electroencephalographic Artifacts by Blind Source Separation

Jurkiewicz, M. T., Gaetz, W. C., Bostan, A. C., & Cheyne, D. (2006). Post-movement beta rebound is generated in motor cortex: evidence from neuromagnetic recordings. *Neuroimage, 32*(3), 1281-1289. doi:10.1016/j.neuroimage.2006.06.005

Kable, J. W., & Glimcher, P. W. (2007). The neural correlates of subjective value during intertemporal choice. *Nat Neurosci, 10*(12), 1625-1633. doi:10.1038/nn2007

Kable, J. W., & Glimcher, P. W. (2009). The neurobiology of decision: consensus and controversy. *Neuron, 63*(6), 733-745. doi:10.1016/j.neuron.2009.09.003

Kahneman, D. (2011). *Thinking, fast and slow*. New York City, United States: Macmillan.

Kahneman, D., & Beatty, J. (1966). Pupil diameter and load on memory. *Sci, 154*(3756), 1583-1585. doi:10.1126/science.154.3756.1583

Kahneman, D., Knetsch, J. L., & Thaler, R. H. (1991). Anomalies: the endowment effect, loss aversion, and status quo bias. *J Econ Perspect, 5*(1), 193-206. doi:10.1257/jep.5.1.193

Kahneman, D., & Tversky, A. (1979). Prospect Theory: An analysis of decision under risk. *J Econometric Soc*, 263-291. doi:10.1142/9789814417358_0006

Kahnt, T., Chang, L. J., Park, S. Q., Heinzle, J., & Haynes, J. D. (2012). Connectivity-based parcellation of the human orbitofrontal cortex. *J Neurosci, 32*(18), 6240-6250. doi:10.1523/jneurosci.0257-12.2012

Kaiser, J., Birbaumer, N., & Lutzenberger, W. (2001). Event-related beta desynchronization indicates timing of response selection in a delayed-response paradigm in humans. *Neurosci Lett, 312*(3), 149-152. doi:10.1016/s0304-3940(01)02217-0

Kaiser, J., Hertrich, I., Ackermann, H., & Lutzenberger, W. (2006). Gamma-band activity over early sensory areas predicts detection of changes in audiovisual speech stimuli. *Neuroimage, 30*(4), 1376-1382. doi:10.1016/j.neuroimage.2005.10.042

Kaiser, J., & Lutzenberger, W. (2005). Cortical oscillatory activity and the dynamics of auditory memory processing. *Rev Neurosci, 16*(3), 239-254. doi:10.1515/REVNEURO.2005.16.3.239

Kaiser, J., Lutzenberger, W., Preissl, H., Mosshammer, D., & Birbaumer, N. (2000). Statistical probability mapping reveals high-frequency magnetoencephalographic activity in supplementary motor area during self-paced finger movements. *Neurosci Lett, 283*(1), 81-84. doi:10.1016/s0304-3940(00)00921-6

Kaiser, J., Ripper, B., Birbaumer, N., & Lutzenberger, W. (2003). Dynamics of gamma-band activity in human magnetoencephalogram during auditory pattern working memory. *Neuroimage, 20*(2), 816-827. doi:10.1016/s1053-8119(03)00350-1

Kameda, T., Takezawa, M., Tindale, R. S., & Smith, C. M. (2002). Social sharing and risk reduction: exploring a computational algorithm for the psychology of windfall gains. *Evol Hum Behav, 23*(1), 11-33. doi:10.1016/S1090-5138(01)00086-1

Kamp, A., Pfurtscheller, G., Edlinger, G., & da Silva, F. L. (2005). Technological basis of eeg recording. In *Electroencephalography, Basic principles, Clinical applications and related fields* (pp. 127-138). Philadelphia, Pennsylvania, United States: Lippincott Williams & Wilkins.

Kanasewich, E. R. (1981). *Time sequence analysis in geophysics*: University of Alberta.

Kaplan, S., & Berman, M. G. (2010). Directed attention as a common resource for executive functioning and self-regulation. *Perspect Psychol Sci, 5*(1), 43-57. doi:10.1177/1745691609356784

Karakaş, S., & Barry, R. J. (2017). A brief historical perspective on the advent of brain oscillations in the biological and psychological disciplines. *Neurosci Biobehav Rev, 75*, 335-347. doi:10.1016/j.neubiorev.2016.12.009

Karasek, R. A. (1979). Job demands, job decision latitude, and mental strain: Implications for job redesign. *Administrative Sci Quarterly*, 285-308. doi: 10.2307/2392498

Karatekin, C. (2004). A test of the integrity of the components of baddeley's model of working memory in attention-deficit/hyperactivity disorder (ADHD). *J Child Psychol Psychiatry, 45*(5), 912-926. doi:10.1111/j.1469-7610.2004.t01-1-00285.x

Karniski, W., Blair, R. C., & Snider, A. D. (1994). An exact statistical method for comparing topographic maps, with any number of subjects and electrodes. *Brain Topogr, 6*(3), 203-210. doi:10.1007/bf01187710

Kastner, S., & Ungerleider, L. G. (2000). Mechanisms of visual attention in the human Cortex. *Annu Rev Neurosci, 23*, 315-341. doi:10.1146/annurev.neuro.23.1.315

Kaufman, B. E. (1999). Expanding the behavioral foundations of labor economics. *Indus Labor Relat Rev*, 361-392. doi:10.2307/2525140

Kawashima, R., Satoh, K., Itoh, H., Ono, S., Furumoto, S., Gotoh, R., . . . Fukuda, H. (1996). Functional anatomy of GO/NO-GO discrimination and response selection--a PET study in man. *Brain Res*, 728(1), 79-89. doi:10.1016/0006-8993(96)00389-7

Keinrath, C., Wriessnegger, S., Muller-Putz, G. R., & Pfurtscheller, G. (2006). Post-movement beta synchronization after kinesthetic illusion, active and passive movements. *Int J Psychophysiol*, *62*(2), 321-327. doi:10.1016/j.ijpsycho.2006.06.001

Kelly, S. P., Lalor, E. C., Reilly, R. B., & Foxe, J. J. (2006). Increases in alpha oscillatory power reflect an active retinotopic mechanism for distracter suppression during sustained visuospatial attention. *J Neurophysiol*, *95*(6), 3844-3851. doi:10.1152/jn.01234.2005

Kendall, S. B. (1974). Preference for intermittent reinforcement. *J Exp Anal Behav, 21*(3), 463-473. doi:10.1901/jeab.1974.21-463

Kerns, J. G., Cohen, J. D., MacDonald, A. W., 3rd, Cho, R. Y., Stenger, V. A., & Carter, C. S. (2004). Anterior cingulate conflict monitoring and adjustments in control. *Sci, 303*(5660), 1023-1026. doi:10.1126/science.1089910

Kidwell Jr, R. E., & Bennett, N. (1993). Employee propensity to withhold effort: A conceptual model to intersect three avenues of research. *Academy of Management review, 18*(3), 429-456.

Kilavik, B. E., Ponce-Alvarez, A., Trachel, R., Confais, J., Takerkart, S., & Riehle, A. (2012). Context-related frequency modulations of macaque motor cortical

lfp beta oscillations. *Cereb Cortex, 22*(9), 2148-2159. doi:10.1093/cercor/bhr299

Killeen, P. R. (2009). An additive-utility model of delay discounting. *Psychol Rev, 116*(3), 602-619. doi:10.1037/a0016414

Killeen, P. R. (2015). The arithmetic of discounting. *J Exp Anal Behav, 103*(1), 249-259. doi:10.1002/jeab.130

Kilner, J. M., Baker, S. N., Salenius, S., Jousmaki, V., Hari, R., & Lemon, R. N. (1999). Task-dependent modulation of 15-30 hz coherence between rectified EMGs from human hand and forearm muscles. *J Physiol, 516 (Pt 2)*, 559-570. doi:10.1111/j.1469-7793.1999.0559v.x

Kilner, J. M., Bott, L., & Posada, A. (2005). Modulations in the degree of synchronization during ongoing oscillatory activity in the human brain. *Eur J Neurosci, 21*(9), 2547-2554. doi:10.1111/j.1460-9568.2005.04069.x

Kilner, J. M., Friston, K. J., & Frith, C. D. (2007). Predictive coding: an account of the mirror neuron system. *Cogn Process, 8*(3), 159-166. doi:10.1007/s10339-007-0170-2

Kilner, J. M., Salenius, S., Baker, S. N., Jackson, A., Hari, R., & Lemon, R. N. (2003). Task-dependent modulations of cortical oscillatory activity in human subjects during a bimanual precision grip task. *Neuroimage, 18*(1), 67-73. doi:10.1006/nimg.2002.1322

Kimberg, D. Y., D'Esposito, M., & Farah, M. J. (1997). Effects of bromocriptine on human subjects depend on working memory capacity. *Neuroreport, 8*(16), 3581-3585.

Kirby, K. N. (1997). Bidding on the future: evidence against normative discounting of delayed rewards. *J Experiment Psychol, 126*(1), 54. doi:10.1037/0096-3445.126.1.54

Kirby, K. N. (2009). One-year temporal stability of delay-discount rates. *Psychon Bull Rev, 16*(3), 457-462. doi:10.3758/pbr.16.3.457

Kirby, K. N., Petry, N. M., & Bickel, W. K. (1999). Heroin addicts have higher discount rates for delayed rewards than non-drug-using controls. *J Exp Psychol Gen, 128*(1), 78-87.

Kivetz, R. (2003). The effects of effort and intrinsic motivation on risky choice. *Market Sci, 22*(4), 477-502. doi:10.1287/mksc.22.4.477.24911

Klass, D. W., & Bickford, R. G. (1957). *Observations on the rolandic arceau rhythm.* Paper presented at the Electroencephalography and clinical neurophysiology.

Klein, C., Wendling, K., Huettner, P., Ruder, H., & Peper, M. (2006). Intra-subject variability in attention-deficit hyperactivity disorder. *Biol Psychiatry, 60*(10), 1088-1097. doi:10.1016/j.biopsych.2006.04.003

Klein-Flügge, M., C., Kennerley, S., W., Saraiva, A., C., Penny, W., D., & Bestmann, S. (2015). Behavioral modeling of human choices reveals dissociable effects of physical effort and temporal delay on reward devaluation. *PLoS Comput Biol,* 11(3), e1004116. doi:10.1371/journal.pcbi.1004116

Klem, G. H., Luders, H. O., Jasper, H. H., & Elger, C. (1999). The ten-twenty electrode system of the international federation. the international federation of Clinical Neurophysiology. *Electroencephalogr Clin Neurophysiol Suppl, 52,* 3-6.

Klimesch, W. (1996). Memory processes, brain oscillations and eeg synchronization. *Internat J Psychophysiol, 24*(1-2), 61-100. doi:10.1016/S0167-8760(96)00057-8

Klimesch, W. (1999). EEG alpha and theta oscillations reflect cognitive and memory performance: a review and analysis. *Brain research reviews, 29*(2-3), 169-195.

Klimesch, W. (1999). EEG alpha and theta oscillations reflect cognitive and memory performance: a review and analysis. *Brain Res Brain Res Rev, 29*(2-3), 169-195. doi:10.1016/S0165-0173(98)00056-3

Klimesch, W. (2012a). Alpha-band oscillations, attention, and controlled access to stored information. *Trends Cog Sci, 16*(12), 606-617. doi:10.1016/j.tics.2012.10.007

Klimesch, W. (2012b). α-band oscillations, attention, and controlled access to stored information. *Trends Cogn Sci, 16*(12), 606-617. doi:10.1016/j.tics.2012.10.007

Klimesch, W., Doppelmayr, M., Schwaiger, J., Auinger, P., & Winkler, T. (1999). 'Paradoxical' alpha synchronization in a memory task. *Brain Res Cogn Brain Res, 7*(4), 493-501. doi:10.1016/S0926-6410(98)00056-1

Klimesch, W., Sauseng, P., & Hanslmayr, S. (2007). EEG alpha oscillations: the inhibition-timing hypothesis. *Brain Res Rev, 53*(1), 63-88. doi:10.1016/j.brainresrev.2006.06.003

Klimesch, W., Schack, B., & Sauseng, P. (2005). The functional significance of theta and upper alpha oscillations. Exp Psychol, 52(2), 99-108. doi:10.1027/1618-3169.52.2.99

Klostermann, F., Nikulin, V. V., Kuhn, A. A., Marzinzik, F., Wahl, M., Pogosyan, A., . . . Curio, G. (2007). Task-related differential dynamics of EEG alpha- and beta-band synchronization in cortico-basal motor structures. *Eur J Neurosci, 25*(5), 1604-1615. doi:10.1111/j.1460-9568.2007.05417.x

Knutson, B., Fong, G. W., Adams, C. M., Varner, J. L., & Hommer, D. (2001). Dissociation of reward anticipation and outcome with event-related fMRI. *Neuroreport, 12*(17), 3683-3687.

Knutson, B., & Greer, S. M. (2008). Anticipatory affect: neural correlates and consequences for choice. *Biolog Sci, 363*(1511), 3771-3786. doi:10.1098/rstb.2008.0155

Knutson, B., Westdorp, A., Kaiser, E., & Hommer, D. (2000). FMRI visualization of brain activity during a monetary incentive delay task. *Neuroimage, 12*(1), 20-27. doi:10.1006/nimg.2000.0593

Koelewijn, T., van Schie, H. T., Bekkering, H., Oostenveld, R., & Jensen, O. (2008). Motor-cortical beta oscillations are modulated by correctness of observed action. *Neuroimage, 40*(2), 767-775. doi:10.1016/j.neuroimage.2007.12.018

Kolev, V., Yordanova, J., Schürmann, M., & Baţar, E. (1999). Event-related alpha oscillations in task processing. Clin Neurophysiol, 110(10), 1784-1792. doi:10.1016/s1388-2457(99)00105-4

Kollenbaum, V. E., Dahme, B., & Kirchner, G. (1996). 'Interoception' of heart rate, blood pressure, and myocardial metabolism during ergometric work load in healthy young subjects. *Biol Psychol,* 42(1-2), 183-197. doi:10.1016/0301-0511(95)05154-6

Kollenbaum, V. E., Dahme, B., Kirchner, G., Katenkamp, B., & Wagner, C. (1994). Assessment of current cardiovascular stress in healthy, young people. *Exp Ange Psycho*l, 41(1), 78-97.

Konishi, S., Nakajima, K., Uchida, I., Sekihara, K., & Miyashita, Y. (1998). No-Go dominant brain activity in human inferior prefrontal cortex revealed by functional magnetic resonance imaging. *Eur J Neurosci*, 10(3), 1209-1213. doi:10.1046/j.1460-9568.1998.00167.x

Konovalov, A., & Krajbich, I. (2019). Over a decade of neuroeconomics: what have we learned? *Organ Res Meth*, 22(1), 148-173. doi:10.1177/1094428116644502

Konorski, J. (1967). Integrative activity of the brain; an interdisciplinary approach. *Cambr Univ Press*. doi:10.1192/bjp.114.514.1185

Koob, G. F., & Le Moal, M. (2008). Review. Neurobiological mechanisms for opponent motivational processes in addiction. *Philos Trans R Soc Lond B Biol Sci*, 363(1507), 3113-3123. doi:10.1098/rstb.2008.0094

Kool, W., & Botvinick, M. (2013). The intrinsic cost of cognitive control. *Behav Brain Sci, 36*(6), 697-698; discussion 707-626. doi:10.1017/s0140525x1300109x

Kool, W., & Botvinick, M. (2014). A labor/leisure tradeoff in cognitive control. *J Exp Psychol Gen, 143*(1), 131-141. doi:10.1037/a0031048

Kool, W., McGuire, J. T., Rosen, Z. B., & Botvinick, M. M. (2010). Decision making and the avoidance of cognitive demand. *J Exp Psychol Gen, 139*(4), 665-682. doi:10.1037/a0020198

Kool, W., Shenhav, A., & Botvinick, M. M. (2017). Cognitive Control as Cost-Benefit Decision Making. *Wiley Handb Cogn Cont*, 167-189. doi:10.1002/9781118920497.ch10

Kopell, N., Ermentrout, G. B., Whittington, M. A., & Traub, R. D. (2000). Gamma rhythms and beta rhythms have different synchronization properties. *Proc Natl Acad Sci, 97*(4), 1867-1872. doi:10.1073/pnas.97.4.1867

Korzhik, O., Morenko, A., & Kotsan, I. Y. (2018). Event-related EEG synchronization/desynchronization under conditions of cessation and switching over of the programs of manual movements in men. *Neurophysiology, 50*(3), 189-197. doi:10.1007/s11062-018-9754-y.

Kösem, A., Gramfort, A., & van Wassenhove, V. (2014). Encoding of event timing in the phase of neural oscillations. *Neuroimage, 92*, 274-284. doi:10.1016/j.neuroimage.2014.02.010

Koyama, K., Hirasawa, H., Okubo, Y., & Karasawa, A. (1997). Quantitative EEG correlates of normal aging in the elderly. *Clin Electroencephalogr*, 28(3), 160-165. doi:10.1177/155005949702800308

Kozlik, J., Neumann, R., & Lozo, L. (2015). Contrasting motivational orientation and evaluative coding accounts: on the need to differentiate the effectors of approach/avoidance responses. *Front Psychol*, 6, 563. doi:10.3389/fpsyg.2015.00563

Krank, M. D. (1985). Asymmetrical effects of pavlovian excitatory and inhibitory aversive transfer on pavlovian appetitive responding and acquisition. *Learning and Motivation, 16*(1), 35-62. doi:10.1016/0023-9690(85)90003-7

Krause, C. M., Lang, H., Laine, M., Kuusisto, M., & Porn, B. (1995). Cortical processing of vowels and tones as measured by event-related desynchronization. *Brain Topogr, 8*(1), 47-56. doi:10.1007/BF01187669

Krawczyk, D. C., Gazzaley, A., & D'Esposito, M. (2007). Reward modulation of prefrontal and visual association cortex during an incentive working memory task. *Brain Res, 1141*, 168-177. doi:10.1016/j.brainres.2007.01.052

Krebs, R. M., Boehler, C. N., & Woldorff, M. G. (2010). The influence of reward associations on conflict processing in the Stroop task. *Cogn*, 117(3), 341-347. doi:10.1016/j.cognition.2010.08.018

Krebs, R. M., & Woldorff, M. G. (2017). Cognitive Control and Reward. *Wiley Handb Cogn Control*, 422-439. doi:10.1002/9781118920497.ch24

Kristjansson, A., Sigurjonsdottir, O., & Driver, J. (2010). Fortune and reversals of fortune in visual search: reward contingencies for pop-out targets affect search efficiency and target repetition effects. *Atten Percept Psychophys, 72*(5), 1229-1236. doi:10.3758/app.72.5.1229

Kruglanski, A. W., Chernikova, M., Rosenzweig, E., & Kopetz, C. (2014). On motivational readiness. Psychol Rev, 121(3), 367-388. doi:10.1037/a0037013

Kuhl, J. (1985). Volitional mediators of cognition-behavior consistency: Self-regulatory processes and action versus state orientation. In Action control (pp. 101-128): Springer.

Kuhn, A. A., Williams, D., Kupsch, A., Limousin, P., Hariz, M., Schneider, G. H., . . . Brown, P. (2004). Event-related beta desynchronization in human subthalamic nucleus correlates with motor performance. *Brain, 127*(Pt 4), 735-746. doi:10.1093/brain/awh106

Kuipers, M., Richter, M., Scheepers, D., Immink, M. A., Sjak-Shie, E., & van Steenbergen, H. (2017). How effortful is cognitive control? Insights from a novel method measuring single-trial evoked beta-adrenergic cardiac reactivity. *Int J Psychophysiol*, 119, 87-92. doi:10.1016/j.ijpsycho.2016.10.007

Kukla, A. (1972). Foundations of an attributional theory of performance. *Psychol Rev*, 79(6), 454.

Kurniawan, I. T., Guitart-Masip, M., & Dolan, R. J. (2011). Dopamine and effort-based decision making. *Front Neurosci, 5*, 81. doi:10.3389/fnins.2011.00081

Kurniawan, I. T., Seymour, B., Talmi, D., Yoshida, W., Chater, N., & Dolan, R. J. (2010). Choosing to make an effort: the role of striatum in signaling physical effort of a chosen action. *J Neurophysiol*, 104(1), 313-321. doi:10.1152/jn.00027.2010

Kurzban, R. (2010). Does the brain consume additional glucose during self-control tasks? *Evol Psychol, 8*(2), 244-259. doi:10.1177/147470491000800208

Kurzban, R. (2016). The sense of effort. *Curr Opin Psychol, 7*, 67-70. doi:10.1016/j.copsyc.2015.08.003

Kurzban, R., Duckworth, A., Kable, J. W., & Myers, J. (2013). An opportunity cost model of subjective effort and task performance. *Behav Brain Sci, 36*(6), 661-679. doi:10.1017/s0140525x12003196

Labyt, E., Cassim, F., Szurhaj, W., Bourriez, J. L., & Derambure, P. (2006). Oscillatory cortical activity related to voluntary muscle relaxation: influence of normal aging. *Clin Neurophysiol*, 117(9), 1922-1930. doi:10.1016/j.clinph.2006.05.017

Laeng, B., Ørbo, M., Holmlund, T., & Miozzo, M. (2011). Pupillary Stroop effects. *Cogn Process*, 12(1), 13-21. doi:10.1007/s10339-010-0370-z

Lammel, S., Ion, D. I., Roeper, J., & Malenka, R. C. (2011). Projection-specific modulation of dopamine neuron synapses by aversive and rewarding stimuli. *Neuron, 70*(5), 855-862. doi:10.1016/j.neuron.2011.03.025

Lampropoulou, S., & Nowicky, A. V. (2012). Evaluation of the numeric rating scale for perception of effort during isometric elbow flexion exercise. *Eur J Appl Physiol*, 112(3), 1167-1175. doi:10.1007/s00421-011-2074-1

Lane, R. E. (1992). Work as "disutility" and money as "happiness": cultural origins of a basic market error. *J Socio-Econ, 21*(1), 43-64. doi:10.1016/1053-5357(92)90025-3

Lang, P. J. (1995). The emotion probe. studies of motivation and attention. *Am Psychol, 50*(5), 372-385. doi:10.1037//0003-066x.50.5.372

Lang, P. J., Bradley, M. M., & Cuthbert, B. N. (1997). Motivated attention: affect, activation, and action. *Atten Orienting, 97*, 135.

Lang, P. J., & Cuthbert, B. N. (1990). Emotion, attention, and the startle reflex. *Psychol Rev, 97*(3), 377.

Lang, P. J., Greenwald, M. K., Bradley, M. M., & Hamm, A. O. (1993). Looking at pictures: affective, facial, visceral, and behavioral reactions. *Psychophysiol, 30*(3), 261-273. doi:0.1111/j.1469-8986.1993.tb03352.x

Langner, R., Sternkopf, M. A., Kellermann, T. S., Grefkes, C., Kurth, F., Schneider, F., . . . Eickhoff, S. B. (2014). Translating working memory into action: behavioral and neural evidence for using motor representations in encoding visuo-spatial sequences. *Hum Brain Mapp, 35*(7), 3465-3484. doi:10.1002/hbm.22415

Lavallee, C. F., Meemken, M. T., Herrmann, C. S., & Huster, R. J. (2014). When holding your horses meets the deer in the headlights: time-frequency characteristics of global and selective stopping under conditions of proactive and reactive control. *Front Hum Neurosci*, 8, 994. doi:10.3389/fnhum.2014.00994

Lazarus, R. S. (1993). From psychological stress to the emotions: a history of changing outlooks. *Annu Rev Psychol, 44*, 1-21. doi:10.1146/annurev.ps.44.020193.000245

Le Bouc, R., Rigoux, L., Schmidt, L., Degos, B., Welter, M. L., Vidailhet, M., . . . Pessiglione, M. (2016). Computational Dissection of Dopamine Motor and Motivational Functions in Humans. *J Neurosci*, 36(25), 6623-6633. doi:10.1523/jneurosci.3078-15.2016

Lebreton, M., Jorge, S., Michel, V., Thirion, B., & Pessiglione, M. (2009). An automatic valuation system in the human brain: evidence from functional neuroimaging. *Neuron, 64*(3), 431-439. doi:10.1016/j.neuron.2009.09.040

LeDoux, J. E. (1997). The emotional brain: the mysterious underpinnings of emotional life. *World and I, 12*, 281-285.

LeDoux, J. E. (2000). Emotion circuits in the brain. *Annu Rev Neurosci*, 23, 155-184. doi:10.1146/annurev.neuro.23.1.155

Lehmann, D. (1984). EEG assessment of brain activity: spatial aspects, segmentation and imaging. *Int J Psychophysiol, 1*(3), 267-276. doi:10.1016/0167-8760(84)90046-1

Leimkuhler, M., & Mesulam, M. M. (1985). Reversible go–no go deficits in a case of frontal lobe tumor. *Annals of neurology, 18*(5), 617-619.

Leknes, S., & Tracey, I. (2008). A common neurobiology for pain and pleasure. *Nat Rev Neurosci, 9*(4), 314-320. doi:10.1038/nrn2333

Lent, R., Azevedo, F. A., Andrade-Moraes, C. H., & Pinto, A. V. (2012). How many neurons do you have? some dogmas of quantitative neuroscience under revision. *Eur J Neurosci, 35*(1), 1-9. doi:10.1111/j.1460-9568.2011.07923.x

Leocani, L., Toro, C., Manganotti, P., Zhuang, P., & Hallett, M. (1997). Event-related coherence and event-related desynchronization/synchronization in the 10 hz and 20 Hz EEG during self-paced movements. *Electroencephalogr Clin Neurophysiol, 104*(3), 199-206. doi:10.1016/S0168-5597(96)96051-7

Leocani, L., Toro, C., Zhuang, P., Gerloff, C., & Hallett, M. (2001). Event-related desynchronization in reaction time paradigms: a comparison with event-related potentials and corticospinal excitability. *Clin Neurophysiol, 112*(5), 923-930. doi:10.1016/s1388-2457(01)00530-2

Levy, J., S. (1992). An introduction to prospect theory. *Polit Psychol*, 171-186. doi: 3791677

Lewin, K., Dembo, T., Festinger, L., & Sears, P., S. (1944). Level of aspiration.

Lewis, M. (1964). Effect of Effort on Value: an Exploratory Study of Children. *Child Dev*, 35, 1337-1342. doi:10.1111/j.1467-8624.1964.tb05271.x

Lezak, M. D., Howieson, D. B., Loring, D. W., & Fischer, J. S. (2004). *Neuropsychological assessment*: Oxford University Press, USA.

Libedinsky, C., Massar, S. A., Ling, A., Chee, W., Huettel, S. A., & Chee, M. W. (2013). Sleep deprivation alters effort discounting but not delay discounting of monetary rewards. *Sleep, 36*(6), 899-904. doi:10.5665/sleep.2720

Liebrand, M., Pein, I., Tzvi, E., & Krämer, U. M. (2017). Temporal dynamics of proactive and reactive motor inhibition. *Front Hum Neurosci,* 11, 204. doi:10.3389/fnhum.2017.00204

Liddle, E. B., Price, D., Palaniyappan, L., Brookes, M. J., Robson, S. E., Hall, E. L., . . . Liddle, P. F. (2016). Abnormal salience signaling in schizophrenia: the role of integrative beta oscillations. *Hum Brain Mapp, 37*(4), 1361-1374. doi:10.1002/hbm.23107

Liley, D. T., Cadusch, P. J., Gray, M., & Nathan, P. J. (2003). Drug-induced modification of the system properties associated with spontaneous human electroencephalographic activity. *Phys Rev E Stat Nonlin Soft Matter Phys, 68*(5 Pt 1), 051906. doi:10.1103/PhysRevE.68.051906

Lin, C. L., Jung, M., Wu, Y. C., Lin, C. T., & She, H. C. (2012). Brain dynamics of mathematical problem solving. Annu Int Conf IEEE Eng Med Biol Soc, 2012, 4768-4771. doi:10.1109/embc.2012.6347033

Lindquist, G. S. (2010). Tournaments and unfair treatment. *J Socio-Econ, 39*(6), 670-682. doi:10.1016/j.socec.2010.06.001

Link, C. G., Leigh, T. J., & Fell, G. L. (1991). Effects of granisetron and lorazepam, alone and in combination, on the EEG of human volunteers. *Br J Clin Pharmacol, 31*(1), 93-97. doi:10.1111/j.1365-2125.1991.tb03863.x

Little, S., Bonaiuto, J., Barnes, G., & Bestmann, S. (2018). Motor cortical beta transients delay movement initiation and track errors. *bioRxiv*, 384370. doi:10.1371/journal.pbio.3000479

Liu, X., Hairston, J., Schrier, M., & Fan, J. (2011). Common and distinct networks underlying reward valence and processing stages: a meta-analysis of

functional neuroimaging studies. *Neurosci Biobehav Rev*, 35(5), 1219-1236. doi:10.1016/j.neubiorev.2010.12.012

Locke, E. A., & Latham, G. P. (1990). A theory of goal setting & task performance: Prentice-Hall, Inc.

Locke, H. S., & Braver, T. S. (2008). Motivational influences on cognitive control: behavior, brain activation, and individual differences. *Cogn Affect Behav Neurosci, 8*(1), 99-112. doi:10.3758/CABN.8.1.99

Locke, H. S., & Braver, T. S. (2008). Motivational influences on cognitive control: behavior, brain activation, and individual differences. *Cogn Affect Behav Neurosci*, 8(1), 99-112. doi:10.3758/CABN.8.1.99

Locke, H. S., & Braver, T. S. (2010). Motivational influences on cognitive control: a cognitive neuroscience perspective. *Self Control Soc*, 114-140.

Loewenstein, G., Rick, S., & Cohen, J. D. (2008). Neuroeconomics. *Annu Rev Psychol, 59*, 647-672. doi:10.1146/annurev.psych.59.103006.093710

Logan, G. D. (1986). Dependence and independence in responding to double stimulation: a comparison of stop, change, and dual-task paradigms. *J Exp Psychol: Hum Percept Performance, 12*(4), 549. doi:10.1037/0096-1523.12.4.549

Logan, G. D. (1994). On the ability to inhibit thought and action: A users' guide to the stop signal paradigm.

Logan, G. D., & Cowan, W. B. (1984). On the ability to inhibit thought and action: a theory of an act of control. *Psychol Rev, 91*(3), 295. doi:10.1037/0033-295X.91.3.295

Logan, G. D., Cowan, W. B., & Davis, K. A. (1984). On the ability to inhibit simple and choice reaction time responses: a model and a method. *J Exp Psychol Hum Percept Perform, 10*(2), 276-291.

Logan, G. D., Van Zandt, T., Verbruggen, F., & Wagenmakers, E. J. (2014). On the ability to inhibit thought and action: general and special theories of an act of control. *Psychol Rev,* 121(1), 66-95. doi:10.1037/a0035230

Logothetis, N. K. (2003). The underpinnings of the bold functional magnetic resonance imaging signal. *J Neurosci, 23*(10), 3963-3971. doi:10.1523/jneurosci.23-10-03963.2003

Lopes da Silva, F. (1991). Neural mechanisms underlying brain waves: from neural membranes to networks. *Electroencephalogr Clin Neurophysiol, 79*(2), 81-93. doi:10.1016/0013-4694(91)90044-5

Lopes da Silva, F., Vos, J. E., Mooibroek, J., & Van Rotterdam, A. (1980). Relative contributions of intracortical and thalamo-cortical processes in the generation of alpha rhythms, revealed by partial coherence analysis. *Electroencephalogr Clin Neurophysiol, 50*(5-6), 449-456. doi:10.1016/0013-4694(80)90011-5

Low, A., Lang, P. J., Smith, J. C., & Bradley, M. M. (2008). Both predator and prey: emotional arousal in threat and reward. *Psychol Sci, 19*(9), 865-873. doi:10.1111/j.1467-9280.2008.02170.x

Lozano-Soldevilla, D., ter Huurne, N., Cools, R., & Jensen, O. (2014). GABAergic modulation of visual gamma and alpha oscillations and its consequences for working memory performance. *Curr Biol, 24*(24), 2878-2887. doi:10.1016/j.cub.2014.10.017

Luce, R., D. (1986). *Response times: Their role in inferring elementary mental organization*: Oxford University Press on Demand.

Luck, S. J. (2005). Ten simple rules for designing ERP experiments. *Event-related potentials: A methods handbook, 262083337*.

Luck, S. J., Woodman, G. F., & Vogel, E. K. (2000). Event-related potential studies of attention. *Trends Cogn Sci, 4*(11), 432-440. doi:10.1016/s1364-6613(00)01545-x

Ludowig, E., Moller, J., Bien, C. G., Munte, T. F., Elger, C. E., & Rosburg, T. (2010). Active suppression in the mediotemporal lobe during directed forgetting. *Neurobiol Learn Mem, 93*(3), 352-361. doi:10.1016/j.nlm.2009.12.001

Luft, C. D., Takase, E., & Darby, D. (2009). Heart rate variability and cognitive function: effects of physical effort. *Biol Psychol*, 82(2), 164-168. doi:10.1016/j.biopsycho.2009.07.007

Luna, B., Marek, S., Larsen, B., Tervo-Clemmens, B., & Chahal, R. (2015). An Integrative model of the maturation of cognitive control. *Annu Rev Neurosci, 38*, 151-170. doi:10.1146/annurev-neuro-071714-034054

Lundqvist, M., Herman, P., & Lansner, A. (2011). Theta and gamma power increases and alpha/beta power decreases with memory load in an attractor network model. J Cogn Neurosci, 23(10), 3008-3020. doi:10.1162/jocn_a_00029

Lutzenberger, W., Ripper, B., Busse, L., Birbaumer, N., & Kaiser, J. (2002). Dynamics of gamma-band activity during an audiospatial working memory task in humans. *J Neurosci, 22*(13), 5630-5638. doi:20026570

MacKay, W. A., & Mendonca, A. J. (1995). Field potential oscillatory bursts in parietal cortex before and during reach. *Brain Res, 704*(2), 167-174. doi:10.1016/0006-8993(95)01109-9

MacLeod, C. M., Dodd, M. D., Sheard, E. D., Wilson, D. A., & Bibi, U. (2003). In opposition to inhibition. *Psychol Learning Mot, 43*, 163-215.

Madden, G. J., & Bickel, W. K. (2010). *Impulsivity: the behavioral and neurological science of discounting*. Worcester, Massachusetts, United States: American Psychological Association.

Madden, G. J., Petry, N. M., & Johnson, P. S. (2009). Pathological gamblers discount probabilistic rewards less steeply than matched controls. *Exp Clin Psychopharmacol, 17*(5), 283-290. doi:10.1037/a0016806

Maddox, W. T., Baldwin, G. C., & Markman, A. B. (2006). A test of the regulatory fit hypothesis in perceptual classification learning. *Mem Cognit, 34*(7), 1377-1397. doi:10.3758/bf03195904

Maes, C., Gooijers, J., Orban de Xivry, J. J., Swinnen, S. P., & Boisgontier, M. P. (2017). Two hands, one brain, and aging. *Neurosci Biobehav Rev*, 75, 234-256. doi:10.1016/j.neubiorev.2017.01.052

Makeig, S. (1993). Auditory event-related dynamics of the eeg spectrum and effects of exposure to tones. *Electroencephalogr Clin Neurophysiol, 86*(4), 283-293. doi:10.1016/0013-4694(93)90110-h

Makeig, S., Debener, S., Onton, J., & Delorme, A. (2004). Mining event-related brain dynamics. *Trends Cogn Sci, 8*(5), 204-210. doi:10.1016/j.tics.2004.03.008

Makeig, S., Delorme, A., Westerfield, M., Jung, T. P., Townsend, J., Courchesne, E., & Sejnowski, T. J. (2004). Electroencephalographic brain dynamics following manually responded visual targets. *PLoS Biol, 2*(6), e176. doi:10.1371/journal.pbio.0020176

Mallat, S. G. (1989). A theory for multiresolution signal decomposition: the wavelet representation. *IEEE Trans Pattern An Mach Intell*, 11(7), 674-693. doi:10.1109/34.192463

Manohar, S. G., Chong, T. T., Apps, M. A., Batla, A., Stamelou, M., Jarman, P. R., . . . Husain, M. (2015). Reward pays the cost of noise reduction in motor and cognitive control. *Curr Biol, 25*(13), 1707-1716. doi:10.1016/j.cub.2015.05.038

Mantini, D., Perrucci, M. G., Del Gratta, C., Romani, G. L., & Corbetta, M. (2007). Electrophysiological signatures of resting state networks in the human brain. *Proc Natl Acad Sci U S A, 104*(32), 13170-13175. doi:10.1073/pnas.0700668104

March, J. G. (1978). Bounded rationality, ambiguity, and the engineering of choice. *Bell J Econ*, 587-608. doi:10.2307/3003600

Maris, E. (2004). Randomization tests for ERP topographies and whole spatiotemporal data matrices. *Psychophysiol, 41*(1), 142-151. doi:10.1111/j.1469-8986.2003.00139.x

Maris, E., & Oostenveld, R. (2007). Nonparametric statistical testing of EEG- and MEG-data. *J Neurosci Methods, 164*(1), 177-190. doi:10.1016/j.jneumeth.2007.03.024

Markman, A. B., & Brendl, C. M. (2005). Constraining theories of embodied cognition. *Psychol Sci, 16*(1), 6-10. doi:10.1111/j.0956-7976.2005.00772.x

Maruo, Y., Schacht, A., Sommer, W., & Masaki, H. (2016). Impacts of motivational valence on the error-related negativity elicited by full and partial errors. *Biol Psychol, 114*, 108-116. doi:10.1016/j.biopsycho.2015.12.004

Massar, S. A., Libedinsky, C., Weiyan, C., Huettel, S. A., & Chee, M. W. (2015). Separate and overlapping brain areas encode subjective value during delay and effort discounting. *Neuroimage, 120*, 104-113. doi:10.1016/j.neuroimage.2015.06.080

Massar, S. A., Lim, J., & Huettel, S. A. (2019). Sleep deprivation, effort allocation and performance. In *Progress in brain research* (Vol. 246, pp. 1-26). Amsterdam, Netherlands: Elsevier.

Massar, S. A., Lim, J., Sasmita, K., & Chee, M. W. (2016). Rewards boost sustained attention through higher effort: a value-based decision making approach. *Biol Psychol, 120*, 21-27. doi:10.1016/j.biopsycho.2016.07.019

Massar, S. A., Lim, J., Sasmita, K., & Chee, M. W. (2019). Sleep deprivation increases the costs of attentional effort: performance, preference and pupil size. *Neuropsychologia, 123*, 169-177. doi:10.1016/j.neuropsychologia.2018.03.032

Matelli, M., Rizzolatti, G., Bettinardi, V., Gilardi, M. C., Perani, D., Rizzo, G., & Fazio, F. (1993). Activation of precentral and mesial motor areas during the execution of elementary proximal and distal arm movements: a PET study. *Neuroreport, 4*(12), 1295-1298. doi:10.1097/00001756-199309150-00002

Mathewson, K. E., Gratton, G., Fabiani, M., Beck, D. M., & Ro, T. (2009). To see or not to see: prestimulus α phase predicts visual awareness. *J Neurosci, 29*(9), 2725-2732.

Mathewson, K. E., Lleras, A., Beck, D. M., Fabiani, M., Ro, T., & Gratton, G. (2011). Pulsed out of awareness: EEG alpha oscillations represent a pulsed-inhibition of ongoing cortical processing. *Front Psychol, 2*, 99. doi:10.3389/fpsyg.2011.00099

Matzke, D., Verbruggen, F., & Logan, G. D. (2018). The stop-signal paradigm. *Stevens' Handbook of Experimental Psychology and Cognitive Neuroscience, 5*, 1-45.

Mazaheri, A., & Jensen, O. (2010). Rhythmic pulsing: linking ongoing brain activity with evoked responses. *Front Hum Neurosci, 4*, 177. doi:10.3389/fnhum.2010.00177

Mazaheri, A., & Picton, T. W. (2005). EEG spectral dynamics during discrimination of auditory and visual targets. Brain Res Cogn Brain Res, 24(1), 81-96. doi:10.1016/j.cogbrainres.2004.12.013

Mazur, J. E. (1987). An adjusting procedure for studying delayed reinforcement. *Commons, ML.; Mazur, JE.; Nevin, JA*, 55-73.

McAllister, C. J., Rönnqvist, K. C., Stanford, I. M., Woodhall, G. L., Furlong, P. L., & Hall, S. D. (2013). Oscillatory beta activity mediates neuroplastic effects of motor cortex stimulation in humans. *J Neurosci, 33*(18), 7919-7927. doi:10.1523/jneurosci.5624-12.2013

McClelland, D., C., Atkinson, J., W., Clark, R., A., & Lowell, E., L. (1953). The achievement motive. New York, 5.

McClure, S. M., Laibson, D. I., Loewenstein, G., & Cohen, J. D. (2004). Separate neural systems value immediate and delayed monetary rewards. *Sci, 306*(5695), 503-507. doi:10.1126/science.1100907

McDermott, T. J., Wiesman, A. I., Proskovec, A. L., Heinrichs-Graham, E., & Wilson, T. W. (2017). Spatiotemporal oscillatory dynamics of visual selective attention during a flanker task. *Neuroimage, 156*, 277-285. doi:10.1016/j.neuroimage.2017.05.014

McCrea, S. M., & Vann, R. J. (2018). Postactional goal pursuit: Consequences of task completion for thought content, affect, and behavioral intentions. *Mot Emot*, 42(6), 852-870. doi:10.1007/s11031-018-9713-3

McEwen, B. S., & Karatsoreos, I. N. (2015). Sleep deprivation and circadian disruption: stress, allostasis, and allostatic load. *Sleep medicine clinics, 10*(1), 1-10. doi:10.1016/j.jsmc.2014.11.007

McFarland, D. J., Miner, L. A., Vaughan, T. M., & Wolpaw, J. R. (2000). Mu and beta rhythm topographies during motor imagery and actual movements. *Brain Topogr, 12*(3), 177-186. doi:10.1023/A:1023437823106

McMahon, C. M., Boisvert, I., de Lissa, P., Granger, L., Ibrahim, R., Lo, C. Y., . . . Graham, P. L. (2016). Monitoring Alpha Oscillations and Pupil Dilation across a Performance-Intensity Function. Front Psychol, 7, 745. doi:10.3389/fpsyg.2016.00745

Medendorp, W. P., Kramer, G. F., Jensen, O., Oostenveld, R., Schoffelen, J. M., & Fries, P. (2007). Oscillatory activity in human parietal and occipital cortex shows hemispheric lateralization and memory effects in a delayed double-step saccade task. *Cereb Cortex, 17*(10), 2364-2374. doi:10.1093/cercor/bhl145

Mega, M. S., & Cummings, J. L. (1997). The cingulate and cingulate syndromes. *Blue Books Practical Neurol, 16*, 189-222.

Mehrabian, A. (1970). A semantic space for nonverbal behavior. *J Consult Clin Psychol, 35*(2), 248. doi:10.1037/h0030083

Mehrabian, A., & Russell, J. A. (1974). *An approach to environmental psychology*. Cambridge, Massachusetts, United States: the MIT Press.

Menon, V., Adleman, N. E., White, C. D., Glover, G. H., & Reiss, A. L. (2001). Error-related brain activation during a Go/NoGo response inhibition task. *Hum Brain Mapp, 12*(3), 131-143. doi:10.1002/1097-0193

Metereau, E., & Dreher, J. C. (2013). Cerebral correlates of salient prediction error for different rewards and punishments. *Cereb Cortex*, 23(2), 477-487. doi:10.1093/cercor/bhs037

Meyer, W. U., & Hallermann, B. (1977). Intended effort and informational value of task outcome. Arch Psychol (Frankf), 129(2), 131-140.

Miall, R. C. (2003). Connecting mirror neurons and forward models. *Neuroreport, 14*(17), 2135-2137. doi:10.1097/01.wnr.0000098751.87269.77

Milad, M. R., & Rauch, S. L. (2012). Obsessive-compulsive disorder: beyond segregated cortico-striatal pathways. *Trends Cogn Sci, 16*(1), 43-51. doi:10.1016/j.tics.2011.11.003

Miller, B. T. (1956). The magical number seven, plus or minus two: some limits on our capacity for processing information. *Psychol Rev, 63*(2), 81. doi:10.1037/h0043158

Miller, B. T. (1999). The prefrontal cortex: complex neural properties for complex behavior. *Neuron, 22*(1), 15-17. doi:S0896-6273(00)80673-X

Miller, B. T. (2007). Theory of the normal waking EEG: from single neurones to waveforms in the alpha, beta and gamma frequency ranges. *Int J Psychophysiol, 64*(1), 18-23. doi:10.1016/j.ijpsycho.2006.07.009

Miller, B. T., & Cohen, J. D. (2001). An integrative theory of prefrontal cortex function. *Annual Rev Neurosci, 24*(1), 167-202. doi:10.1146/annurev.neuro.24.1.167

Miller, B. T., & D'Esposito, M. (2005). Searching for "the top" in top-down control. *Neuron, 48*(4), 535-538. doi:10.1016/j.neuron.2005.11.002

Miller, B. T., Thome, A., & Cowen, S. L. (2013). Intersection of effort and risk: ethological and neurobiological perspectives. *Front Neurosci, 7*, 208. doi:10.3389/fnins.2013.00208

Mitchell, S. H. (1999). Measures of impulsivity in cigarette smokers and non-smokers. *Psychopharmacol, 146*(4), 455-464. doi:10.1007/PL00005491

Mitchell, S. H. (2004). Effects of short-term nicotine deprivation on decision-making: delay, uncertainty and effort discounting. *Nicotine Tob Res, 6*(5), 819-828. doi:10.1080/14622200412331296002

Mitchell, D. J., McNaughton, N., Flanagan, D., & Kirk, I. J. (2008). Frontal-midline theta from the perspective of hippocampal "theta". Prog Neurobiol, 86(3), 156-185. doi:10.1016/j.pneurobio.2008.09.005

Mizuhiki, T., Richmond, B. J., & Shidara, M. (2012). Encoding of reward expectation by monkey anterior insular neurons. *J Neurophysiol*, 107(11), 2996-3007. doi:10.1152/jn.00282.2011

Mochon, D., Norton, M. I., & Ariely, D. (2012). Bolstering and restoring feelings of competence via the IKEA effect. *Internat J Res Market, 29*(4), 363-369. doi:10.1016/j.ijresmar.2012.05.001

Mohr, P. N., Biele, G., & Heekeren, H. R. (2010). Neural processing of risk. *J Neurosci, 30*(19), 6613-6619. doi:10.1523/JNEUROSCI.0003-10.2010

Monterosso, J., & Ainslie, G. (1999). Beyond discounting: possible experimental models of impulse control. *Psychopharmacol, 146*(4), 339-347. doi:10.1007/PL00005480

Morel, P., Ulbrich, P., & Gail, A. (2017). What makes a reach movement effortful? Physical effort discounting supports common minimization principles in decision making and motor control. *PLoS Biol, 15*(6), e2001323. doi:10.1371/journal.pbio.2001323

Mori, H., Takio, K., Ogawara, M., & Selkoe, D. (1992). Mass spectrometry of purified amyloid beta protein in Alzheimer's disease. *J Biol Chem, 267*(24), 17082-17086.

Muehlbacher, S., & Kirchler, E. (2009). Origin of endowments in public good games: the impact of effort on contributions. *J Neurosci Psychol Econ, 2*(1), 59. doi:10.1037/a0015458

Mulholland, T. (1995). Human EEG, behavioral stillness and biofeedback. *Int J Psychophysiol, 19*(3), 263-279. doi:10.1016/0167-8760(95)00019-O

Muraven, M., & Baumeister, R. F. (2000). Self-regulation and depletion of limited resources: does self-control resemble a muscle? *Psychol Bull, 126*(2), 247-259. doi:10.1037/0033-2909.126.2.247

Murthy, V. N., & Fetz, E. E. (1996). Oscillatory activity in sensorimotor cortex of awake monkeys: synchronization of local field potentials and relation to behavior. *J Neurophysiol, 76*(6), 3949-3967. doi:10.1152/jn.1996.76.6.3949

Muthukumaraswamy, S. D., Myers, J. F., Wilson, S. J., Nutt, D. J., Hamandi, K., Lingford-Hughes, A., & Singh, K. D. (2013). Elevating endogenous GABA levels with GAT-1 blockade modulates evoked but not induced responses in human visual cortex. *Neuropsychopharmacol, 38*(6), 1105-1112. doi:10.1038/npp.2013.9

Myerson, J., Green, L., Hanson, J. S., Holt, D. D., & Estle, S. J. (2003). Discounting delayed and probabilistic rewards: processes and traits. *J Econ Psychol, 24*(5), 619-635. doi:10.1016/S0167-4870(03)00005-9

Myerson, J., Green, L., & Morris, J. (2011). Modeling the effect of reward amount on probability discounting. J Exp Anal Behav, 95(2), 175-187. doi:10.1901/jeab.2011.95-175

Myerson, J., Green, L., & Warusawitharana, M. (2001). Area under the curve as a measure of discounting. *J Exp Anal Behav, 76*(2), 235-243. doi:10.1901/jeab.2001.76-235

Naccarato, M., Calautti, C., Jones, P. S., Day, D. J., Carpenter, T. A., & Baron, J. C. (2006). Does healthy aging affect the hemispheric activation balance during paced index-to-thumb opposition task? An fMRI study. *Neuroimage*, 32(3), 1250-1256. doi:10.1016/j.neuroimage.2006.05.003

Nagai, H., & Tanaka, T. (2019). Action observation of own hand movement enhances event-related desynchronization. *IEEE Transactions on Neural Systems and Rehabilitation Engineering*.

Nakagawa, K., Aokage, Y., Fukuri, T., Kawahara, Y., Hashizume, A., Kurisu, K., & Yuge, L. (2011). Neuromagnetic beta oscillation changes during motor imagery and motor execution of skilled movements. *Neuroreport, 22*(5), 217-222. doi:10.1097/WNR.0b013e328344b480

Neuper, C., & Pfurtscheller, G. (2001a). Event-related dynamics of cortical rhythms: frequency-specific features and functional correlates. *Int J Psychophysiol, 43*(1), 41-58. doi:10.1016/s0167-8760(01)00178-7

Neuper, C., & Pfurtscheller, G. (2001b). Evidence for distinct beta resonance frequencies in human eeg related to specific sensorimotor cortical areas. *Clin Neurophysiol, 112*(11), 2084-2097. doi:10.1016/S1388-2457(01)00661-7

Neuper, C., Wortz, M., & Pfurtscheller, G. (2006). ERD/ERS patterns reflecting sensorimotor activation and deactivation. *Prog Brain Res, 159*, 211-222. doi:10.1016/s0079-6123(06)59014-4

Neuper, C., Wörtz, M., & Pfurtscheller, G. (2006). ERD/ERS patterns reflecting sensorimotor activation and deactivation. *Progress in brain research, 159*, 211-222.

Neuringer, A. J. (1967). Effects of reinforcement magnitude on choice and rate of responding. *J Exp Anal Behav, 10*(5), 417-424. doi:10.1901/jeab.1967.10-417

Newlin, D. B., & Levenson, R. W. (1979). Pre-ejection period: measuring beta-adrenergic influences upon the heart. *Psychophysiol*, 16(6), 546-553. doi:10.1111/j.1469-8986.1979.tb01519.x

Nigg, J. T. (2000). On inhibition/disinhibition in developmental psychopathology: views from cognitive and personality psychology and a working inhibition taxonomy. *Psychol Bull, 126*(2), 220-246. doi:10.1037/0033-2909.126.2.220

Nikulin, V. V., Nikulina, A. V., Yamashita, H., Rossi, E. M., & Kähkönen, S. (2005). Effects of alcohol on spontaneous neuronal oscillations: a combined magnetoencephalography and electroencephalography study. *Prog Neuropsychopharmacol Biol Psychiatry, 29*(5), 687-693. doi:10.1016/j.pnpbp.2005.04.014

Nishiyama, R. (2014). Response effort discounts the subjective value of rewards. *Behav Processes, 107*, 175-177. doi:10.1016/j.beproc.2014.08.002

Nishiyama, R. (2016). Physical, emotional, and cognitive effort discounting in gain and loss situations. *Behav Processes, 125*, 72-75. doi:10.1016/j.beproc.2016.02.004

Niv, Y., Daw, N. D., Joel, D., & Dayan, P. (2007). Tonic dopamine: opportunity costs and the control of response vigor. *Psychopharmacol, 191*(3), 507-520. doi:10.1007/s00213-006-0502-4

Noh, N. A., Fuggetta, G., Manganotti, P., & Fiaschi, A. (2012). Long lasting modulation of cortical oscillations after continuous theta burst transcranial magnetic stimulation. *PloS one, 7*(4), e35080. doi:10.1371/journal.pone.0035080

Norman, D., & Shallice, T. (1986). Attention to action: willed and automatic control of behavior", from consciousness and self-regulation: advances in research and theory, Vol. 4, R. Davidson, G. Schwartz, and D. Shapiro. In. New York, United States: Plenum Press.

Norton, M. I., Mochon, D., & Ariely, D. (2012). The IKEA effect: when labor leads to love. *J Cons Psychol, 22*(3), 453-460. doi:10.1016/j.jcps.2011.08.002

Novak, K. D., & Foti, D. (2015). Teasing apart the anticipatory and consummatory processing of monetary incentives: An event-related potential study of reward dynamics. *Psychophysiol*, 52(11), 1470-1482. doi:10.1111/psyp.12504

Nunez, P. L. (2000). Toward a quantitative description of large-scale neocortical dynamic function and EEG. *Behav Brain Sci, 23*(3), 371-398; discussion 399-437. doi:10.1017/S0140525X00243252

Nunez, P. L., & Srinivasan, R. (2006). *Electric fields of the brain: the neurophysics of EEG*. Oxford, United Kingdom: Oxford University Press.

Nunez, P. L., Srinivasan, R., Westdorp, A. F., Wijesinghe, R. S., Tucker, D. M., Silberstein, R. B., & Cadusch, P. J. (1997). EEG coherency. I: Statistics, reference electrode, volume conduction, Laplacians, cortical imaging, and interpretation at multiple scales. *Electroencephalogr Clin Neurophysiol, 103*(5), 499-515. doi:10.1016/s0013-4694(97)00066-7

O'Connell, R. G., Dockree, P. M., Bellgrove, M. A., Kelly, S. P., Hester, R., Garavan, H., . . . Foxe, J. J. (2007). The role of cingulate cortex in the detection of errors with and without awareness: a high-density electrical mapping study. *Eur J Neurosci, 25*(8), 2571-2579. doi:10.1111/j.1460-9568.2007.05477.x

O'Doherty, J. (2004). Reward representations and reward-related learning in the human brain: insights from neuroimaging. *Curr Opin Neurobiol,* 14(6), 769-776. doi:10.1016/j.conb.2004.10.016

O'Reilly, R. C., & Frank, M. J. (2006). Making working memory work: a computational model of learning in the prefrontal cortex and basal ganglia. *Neural Comput, 18*(2), 283-328. doi:10.1162/089976606775093909

Obleser, J., Wöstmann, M., Hellbernd, N., Wilsch, A., & Maess, B. (2012). Adverse listening conditions and memory load drive a common α oscillatory network. J Neurosci, 32(36), 12376-12383. doi:10.1523/jneurosci.4908-11.2012

Obrist, P. A. (2012). Cardiovascular psychophysiology: A perspective: Springer Science & Business Media.

Obrist, P. A. (1976). Presidential Address, 1975. The cardiovascular-behavioral interaction--as it appears today. *Psychophysiol,* 13(2), 95-107. doi:10.1111/j.1469-8986.1976.tb00081.x

Odum, A. L. (2011). Delay discounting: trait variable? *Behav Processes, 87*(1), 1-9. doi:10.1016/j.beproc.2011.02.007

Odum, A. L., Baumann, A. A., & Rimington, D. D. (2006). Discounting of delayed hypothetical money and food: effects of amount. *Behav Processes, 73*(3), 278-284. doi:10.1016/j.beproc.2006.06.008

Ohmura, Y., Takahashi, T., & Kitamura, N. (2005). Discounting delayed and probabilistic monetary gains and losses by smokers of cigarettes. *Psychopharmacol, 182*(4), 508-515. doi:10.1007/s00213-005-0110-8

Okun, M., & Lampl, I. (2008). Instantaneous correlation of excitation and inhibition during ongoing and sensory-evoked activities. *Nat Neurosci, 11*(5), 535-537. doi:10.1038/nn.2105

Olson, E. A., Hooper, C. J., Collins, P., & Luciana, M. (2007). Adolescents' performance on delay and probability discounting tasks: contributions of age, intelligence, executive functioning, and self-reported externalizing behavior. *Pers Individ Dif, 43*(7), 1886-1897. doi:10.1016/j.paid.2007.06.016

Omlor, W., Patino, L., Mendez-Balbuena, I., Schulte-Monting, J., & Kristeva, R. (2011). Corticospinal beta-range coherence is highly dependent on the pre-stationary motor state. *J Neurosci, 31*(22), 8037-8045. doi:10.1523/jneurosci.4153-10.2011

Onoda, K., Okamoto, Y., Shishida, K., Hashizume, A., Ueda, K., Yamashita, H., & Yamawaki, S. (2007). Anticipation of affective images and event-related desynchronization (ERD) of alpha activity: an MEG study. *Brain Res, 1151*, 134-141. doi:10.1016/j.brainres.2007.03.026

Onton, J., Delorme, A., & Makeig, S. (2005). Frontal midline EEG dynamics during working memory. Neuroimage, 27(2), 341-356. doi:10.1016/j.neuroimage.2005.04.014

Oostenveld, R., & Praamstra, P. (2001). The five percent electrode system for high-resolution EEG and ERP measurements. *Clin Neurophysiol, 112*(4), 713-719. doi:10.1016/s1388-2457(00)00527-7

Osgood, C. E. (1952). The nature and measurement of meaning. *Psychol Bull, 49*(3), 197. doi:10.1037/h0055737

Osgood, C. E., Suci, G. J., & Tannenbaum, P. H. (1957). *The measurement of meaning*. Illinois, United States: University of Illinois press.

Ostaszewski, P., Bąbel, P., & Swebodziński, B. (2013). Physical and cognitive effort discounting of hypothetical monetary rewards. *Japanese Psychol Res, 55*(4), 329-337. doi:10.1111/jpr.12019

Othmer, S., Othmer, S. F., & Kaiser, D. A. (1999). EEG biofeedback: An emerging model for its global efficacy. In Introduction to quantitative EEG and neurofeedback (pp. 243-310): Elsevier.

Ott, T., Jacob, S. N., & Nieder, A. (2014). Dopamine receptors differentially enhance rule coding in primate prefrontal cortex neurons. *Neuron, 84*(6), 1317-1328. doi:10.1016/j.neuron.2014.11.012

Otto, A. R., & Daw, N. D. (2019). The opportunity cost of time modulates cognitive effort. *Neuropsychologia, 123*, 92-105. doi:10.1016/j.neuropsychologia.2018.05.006

Padmala, S., & Pessoa, L. (2010). Interactions between cognition and motivation during response inhibition. *Neuropsychologia, 48*(2), 558-565. doi:10.1016/j.neuropsychologia.2009.10.017

Padmala, S., & Pessoa, L. (2011). Reward reduces conflict by enhancing attentional control and biasing visual cortical processing. *J Cog Neurosci, 23*(11), 3419-3432. doi:10.1162/jocn_a_00011

Padoa-Schioppa, C. (2011). Neurobiology of economic choice: a good-based model. *Annu Rev Neurosci, 34*, 333-359. doi:10.1146/annurev-neuro-061010-113648

Palmer, C. E., Davare, M., & Kilner, J. M. (2016). Physiological and perceptual sensory attenuation have different underlying neurophysiological correlates. *J Neurosci*, 36(42), 10803-10812. doi:10.1523/jneurosci.1694-16.2016

Palmer, C. E., Zapparoli, L., & Kilner, J. M. (2016). A new framework to explain sensorimotor beta oscillations. *Trend Cog Sci, 20*(5), 321-323. doi:10.1016/j.tics.2016.03.007

Park, S. Q., Kahnt, T., Rieskamp, J., & Heekeren, H. R. (2011). Neurobiology of value integration: when value impacts valuation. J Neurosci, 31(25), 9307-9314. doi:10.1523/jneurosci.4973-10.2011

Park, D. C., & Reuter-Lorenz, P. A. (2009). The adaptive brain: aging and neurocognitive scaffolding. *Ann Rev Psychol, 60*, 173-196. doi:10.1146/annurev.psych.59.103006.093656

Paschke, L. M., Walter, H., Steimke, R., Ludwig, V. U., Gaschler, R., Schubert, T., & Stelzel, C. (2015). Motivation by potential gains and losses affects control processes via different mechanisms in the attentional network. *Neuroimage, 111*, 549-561. doi:10.1016/j.neuroimage.2015.02.047

Pascual-Marqui, R. D., Michel, C. M., & Lehmann, D. (1994). Low resolution electromagnetic tomography: a new method for localizing electrical activity in the brain. *Int J Psychophysiol, 18*(1), 49-65. doi:10.1016/0167-8760(84)90014-x

Passingham, R. E. (1993). *The frontal lobes and voluntary action*. Oxford, United Kingdom: Oxford University Press.

Patel, K. T., Stevens, M. C., Meda, S. A., Muska, C., Thomas, A. D., Potenza, M. N., & Pearlson, G. D. (2013). Robust changes in reward circuitry during reward loss in current and former cocaine users during performance of a monetary incentive delay task. *Biol Psychiatry, 74*(7), 529-537. doi:10.1016/j.biopsych.2013.04.029

Paus, T., Zatorre, R. J., Hofle, N., Caramanos, Z., Gotman, J., Petrides, M., & Evans, A. C. (1997). Time-related changes in neural systems underlying attention and arousal during the performance of an auditory vigilance task. J Cogn Neurosci, 9(3), 392-408. doi:10.1162/jocn.1997.9.3.392

Peinemann, A., Lehner, C., Conrad, B., & Siebner, H. R. (2001). Age-related decrease in paired-pulse intracortical inhibition in the human primary motor cortex. *Neurosci Lett*, 313(1-2), 33-36. doi:10.1016/s0304-3940(01)02239-x

Pennebaker, J. W. (1981). Stimulus characteristics influencing estimation of heart rate. *Psychophysiol*, 18(5), 540-548. doi:10.1111/j.1469-8986.1981.tb01824.x

Pennebaker, J. W., & Lightner, J. M. (1980). Competition of internal and external information in an exercise setting. *J Pers Soc Psychol*, 39(1), 165-174. doi:10.1037//0022-3514.39.1.165

Perez, M. A., & Cohen, L. G. (2008). Mechanisms underlying functional changes in the primary motor cortex ipsilateral to an active hand. *J Neurosci, 28*(22), 5631-5640. doi:10.1523/jneurosci.0093-08.2008

Pernet, C. R., Latinus, M., Nichols, T. E., & Rousselet, G. A. (2015). Cluster-based computational methods for mass univariate analyses of event-related brain

potentials/fields: A simulation study. *J Neurosci Methods*, 250, 85-93. doi:10.1016/j.jneumeth.2014.08.003

Pesonen, M., Björnberg, C. H., Hämäläinen, H., & Krause, C. M. (2006). Brain oscillatory 1-30 Hz EEG ERD/ERS responses during the different stages of an auditory memory search task. Neurosci Lett, 399(1-2), 45-50. doi:10.1016/j.neulet.2006.01.053

Pessoa, L. (2008). On the relationship between emotion and cognition. *Nat Rev Neurosci*, 9(2), 148-158. doi:10.1038/nrn2317

Pessoa, L. (2009). How do emotion and motivation direct executive control? *Trends Cogn Sci, 13*(4), 160-166. doi:10.1016/j.tics.2009.01.006

Pessoa, L., & Engelmann, J. B. (2010). Embedding reward signals into perception and cognition. *Front Neurosci, 4*. doi:10.3389/fnins.2010.00017

Peters, J., & Buchel, C. (2009). Overlapping and distinct neural systems code for subjective value during intertemporal and risky decision making. *J Neurosci, 29*(50), 15727-15734. doi:10.1523/jneurosci.3489-09.2009

Peters, J., & Büchel, C. (2010). Episodic Future thinking reduces reward delay discounting through an enhancement of prefrontal-mediotemporal interactions. *Neuron, 66*(1), 138-148. doi:10.1016/j.neuron.2010.03.026

Peterson, B. W., Maunz, R. A., Pitts, N. G., & Mackel, R. G. (1975). Patterns of projection and braching of reticulospinal neurons. *Exp Brain Res, 23*(4), 333-351. doi:10.1007/bf00238019

Petry, N. M., & Madden, G. J. (2010). Discounting and pathological gambling. doi:10.1037/12069-010

Pfurtscheller, G. (1977). Graphical display and statistical evaluation of event-related desynchronization (ERD). *Electroencephalogr Clin Neurophysiol, 43*(5), 757-760. doi:10.1016/0013-4694(77)90092-x

Pfurtscheller, G. (1981). Central beta rhythm during sensorimotor activities in man. *Electroencephal Clin Neurophysiol, 51*(3), 253-264. doi:10.1016/0013-4694(81)90139-5

Pfurtscheller, G. (2003). Induced oscillations in the alpha band: functional meaning. *Epilepsia, 44*, 2-8.

Pfurtscheller, G., & Aranibar, A. (1977). Event-related cortical desynchronization detected by power measurements of scalp EEG. *Electroencephalogr Clin Neurophysiol, 42*(6), 817-826. doi:10.1016/0013-4694(77)90235-8

Pfurtscheller, G., & Aranibar, A. (1979). Evaluation of event-related desynchronization (ERD) preceding and following voluntary self-paced movement. *Electroencephalogr Clin Neurophysiol, 46*(2), 138-146. doi:10.1016/0013-4694(79)90063-4

Pfurtscheller, G., & Berghold, A. (1989). Patterns of cortical activation during planning of voluntary movement. *Electroencephalogr Clin Neurophysiol, 72*(3), 250-258. doi:10.1016/0013-4694(89)90250-2

Pfurtscheller, G., Flotzinger, D., & Neuper, C. (1994). Differentiation between finger, toe and tongue movement in man based on 40 Hz EEG. *Electroencephalogr Clin Neurophysiol, 90*(6), 456-460. doi:10.1016/0013-4694(94)90137-6

Pfurtscheller, G., Graimann, B., Huggins, J., Levine, S., & Schuh, L. (2003). Spatiotemporal patterns of beta desynchronization and gamma

synchronization in corticographic data during self-paced movement. *Clin Neurophysiol, 114*(7), 1226-1236. doi:10.1016/S1388-2457(03)00067-1

Pfurtscheller, G., & Klimesch, W. (1992). Functional topography during a visuoverbal judgment task studied with event-related desynchronization Mapping. *J Clin Neurophysiol, 9*(1), 120-131.

Pfurtscheller, G., & Lopes da Silva, F. H. (1999). Event-related EEG/MEG synchronization and desynchronization: basic principles. *Clin Neurophysiol, 110*(11), 1842-1857. doi:10.1016/s1388-2457(99)00141-8

Pfurtscheller, G., & Neuper, C. (1997). Motor imagery activates primary sensorimotor area in humans. *Neurosci Lett, 239*(2-3), 65-68. doi:10.1016/S0304-3940(97)00889-6

Pfurtscheller, G., Neuper, C., Brunner, C., & da Silva, F. L. (2005). Beta rebound after different types of motor imagery in man. *Neurosci Lett, 378*(3), 156-159. doi:10.1016/j.neulet.2004.12.034

Pfurtscheller, G., Neuper, C., & Kalcher, J. (1993). 40-Hz oscillations during motor behavior in man. *Neurosci Lett, 164*(1-2), 179-182. doi:10.1016/0304-3940(93)90886-P

Pfurtscheller, G., Neuper, C., & Krausz, G. (2000). Functional dissociation of lower and upper frequency mu rhythms in relation to voluntary limb movement. *Clin Neurophysiol, 111*(10), 1873-1879.

Pfurtscheller, G., Stancak, A., & Edlinger, G. (1997). On the existence of different types of central beta rhythms below 30 Hz. *Electroencephalo Clin Neurophysiol, 102*(4), 316-325. doi:10.1016/S0013-4694(96)96612-2

Pfurtscheller, G., Stancak, A., Jr., & Neuper, C. (1996). Event-related synchronization (ERS) in the alpha band--an electrophysiological correlate of

cortical idling: a review. *Int J Psychophysiol, 24*(1-2), 39-46. doi:10.1016/S0167-8760(96)00066-9

Pfurtscheller, G., Stancak, A., & Neuper, C. (1996). Post-movement beta synchronization. A correlate of an idling motor area? *Electroencephalogr Clin Neurophysiol, 98*(4), 281-293. doi:10.1016/0013-4694(95)00258-8

Pfurtscheller, G., Stancak Jr, A., & Neuper, C. (1996). Event-related synchronization (ERS) in the alpha band—an electrophysiological correlate of cortical idling: a review. *Internat J Psychophysiol, 24*(1-2), 39-46.

Phaf, R. H., Mohr, S. E., Rotteveel, M., & Wicherts, J. M. (2014). Approach, avoidance, and affect: a meta-analysis of approach-avoidance tendencies in manual reaction time tasks. *Front Psychol*, 5, 378. doi:10.3389/fpsyg.2014.00378

Piai, V., Roelofs, A., & van der Meij, R. (2012). Event-related potentials and oscillatory brain responses associated with semantic and Stroop-like interference effects in overt naming. *Brain Res, 1450*, 87-101. doi:10.1016/j.brainres.2012.02.050

Pichora-Fuller, M. K., Kramer, S. E., Eckert, M. A., Edwards, B., Hornsby, B. W., Humes, L. E., . . . Wingfield, A. (2016). Hearing impairment and cognitive energy: the framework for understanding effortful listening (FUEL). *Ear Hear*, 37 Suppl 1, 5s-27s. doi:10.1097/aud.0000000000000312

Pignatelli, M., & Bonci, A. (2015). Role of dopamine neurons in reward and aversion: a synaptic plasticity perspective. *Neuron, 86*(5), 1145-1157. doi:10.1016/j.neuron.2015.04.015

Pineda, J. A. (2005). The functional significance of mu rhythms: translating “seeing” and “hearing” into “doing”. *Brain Res Rev, 50*(1), 57-68. doi:10.1016/j.brainresrev.2005.04.005

Pintrich, P., R. (2002). *Motivation in education: Theory, research, and applications:* Prentice Hall. Hoboken, New Jersey.

Pistohl, T., Schulze-Bonhage, A., Aertsen, A., Mehring, C., & Ball, T. (2012). Decoding natural grasp types from human ECoG. *Neuroimage, 59*(1), 248-260. doi:10.1016/j.neuroimage.2011.06.084

Pogosyan, A., Gaynor, L. D., Eusebio, A., & Brown, P. (2009). Boosting cortical activity at Beta-band frequencies slows movement in humans. *Curr Biol, 19*(19), 1637-1641. doi:10.1016/j.cub.2009.07.074

Posner, M. I. (1980). Orienting of Attention. *J Exp Psychol, 32*(1), 3-25. doi:10.1080/00335558008248231

Posner, M. I., Snyder, C., & Solso, R. (2004). Attention and cognitive control. *Cog Psychol, 205*.

Possin, K. L., Filoteo, J. V., Song, D. D., & Salmon, D. P. (2009). Space-based but not object-based inhibition of return is impaired in Parkinson's disease. *Neuropsychologia, 47*(7), 1694-1700. doi:10.1016/j.neuropsychologia.2009.02.006

Potma, E. J., Stienen, G. J., Barends, J. P., & Elzinga, G. (1994). Myofibrillar ATPase activity and mechanical performance of skinned fibres from rabbit psoas muscle. *J Physiol,* 474(2), 303-317. doi:10.1113/jphysiol.1994.sp020023

Potts, G. F. (2011). Impact of reward and punishment motivation on behavior monitoring as indexed by the error-related negativity. *Int J Psychophysiol, 81*(3), 324-331. doi:10.1016/j.ijpsycho.2011.07.020

Pratto, F., & John, O. P. (1991). Automatic vigilance: the attention-grabbing power of negative social information. *J Pers Soc Psychol, 61*(3), 380-391. doi:10.1037/0022-3514.61.3.380

Press, W. H., Teukolsky, S. A., Vetterling, W. T., & Flannery, B. P. (1992). Numerical recipes in C++. *The art of scientific computing*, 2, 1002.

Preston, J., Wegner, D., Morsella, E., Bargh, J., & Gollwitzer, P. (2009). *Elbow grease: The experience of effort in action*. In Ezequiel Morsella, John A. Bargh & Peter M. Gollwitzer (eds.), Oxford Handbook of Human Action. Oxford University Press (2009)

Prévost, C., Pessiglione, M., Météreau, E., Cléry-Melin, M., & Dreher, J. C. (2010). Separate valuation subsystems for delay and effort decision costs. *J Neurosci, 30*(42), 14080-14090. doi:10.1523/JNEUROSCI.2752-10.2010

Proskovec, A. L., Heinrichs-Graham, E., Wiesman, A. I., McDermott, T. J., & Wilson, T. W. (2018). Oscillatory dynamics in the dorsal and ventral attention networks during the reorienting of attention. *Hum Brain Mapp, 39*(5), 2177-2190. doi:10.1002/hbm.23997

Rachlin, H. (1990). Why do people gamble and keep gambling despite heavy losses? *Psychol Sci, 1*(5), 294-297. doi:10.1111/j.1467-9280.1990.tb00220.x

Rachlin, H. (2006). Notes on discounting. *J Exp Anal Behav, 85*(3), 425-435. doi:10.1901/jeab.2006.85-05

Rachlin, H., & Green, L. (1972). Commitment, choice and self-control. *J Exp Anal Behav, 17*(1), 15-22. doi:10.1901/jeab.1972.17-15

Rachlin, H., Raineri, A., & Cross, D. (1991). Subjective probability and delay. *J Exp Anal Behav, 55*(2), 233-244. doi:10.1901/jeab.1991.55-233

Rachlin, H., Safin, V., Arfer, K. B., & Yen, M. (2015). The attraction of gambling. *J Exp Anal Behav, 103*(1), 260-266. doi:10.1002/jeab.113

Rachlin, H., & Siegel, E. (1994). Temporal patterning in probabilistic choice. *Organizat Behav Hum Decis Proc*. doi:10.1006/obhd.1994.1054

Raghavachari, S., Lisman, J. E., Tully, M., Madsen, J. R., Bromfield, E. B., & Kahana, M. J. (2006). Theta oscillations in human cortex during a working-memory task: evidence for local generators. *J Neurophysiol, 95*(3), 1630-1638. doi:10.1152/jn.00409.2005

Raichle, M. E., & Mintun, M. A. (2006). Brain work and brain imaging. *Annu Rev Neurosci, 29*, 449-476. doi:10.1146/annurev.neuro.29.051605.112819

Raineri, A., & Rachlin, H. (1993). The effect of temporal constraints on the value of money and other commodities. *J Behav Decis Making, 6*(2), 77-94. doi:10.1002/bdm.3960060202

Rajan, A., Siegel, S. N., Liu, Y., Bengson, J., Mangun, G. R., & Ding, M. (2018). Theta oscillations index frontal decision-making and mediate reciprocal frontal–parietal interactions in willed attention. *Cerebral cortex*.

Randall, W. M., & Smith, J. L. (2011). Conflict and inhibition in the cued-Go/Nogo Task. *Clin Neurophysiol, 122*(12), 2400-2407. doi:10.1016/j.clinph.2011.05.012

Ratcliff, R. (1993). Methods for dealing with reaction time outliers. *Psychol Bull*, 114(3), 510-532. doi:10.1037/0033-2909.114.3.510

Rau, C., Plewnia, C., Hummel, F., & Gerloff, C. (2003). Event-related desynchronization and excitability of the ipsilateral motor cortex during

simple self-paced finger movements. *Clin Neurophysiol, 114*(10), 1819-1826. doi:10.1016/S1388-2457(03)00174-3

Ray, N. J., Brittain, J. S., Holland, P., Joundi, R. A., Stein, J. F., Aziz, T. Z., & Jenkinson, N. (2012). The role of the subthalamic nucleus in response inhibition: evidence from local field potential recordings in the human subthalamic nucleus. *Neuroimage, 60*(1), 271-278. doi:10.1016/j.neuroimage.2011.12.035

Raz, J., Zheng, H., Ombao, H., & Turetsky, B. (2003). Statistical tests for fMRI based on experimental randomization. *Neuroimage, 19*(2 Pt 1), 226-232. doi:10.1016/s1053-8119(03)00115-0

Reynolds, B. (2006). A review of delay-discounting research with humans: relations to drug use and gambling. *Behav Pharmacol, 17*(8), 651-667. doi:10.1097/FBP.0b013e3280115f99

Reynolds, B., Richards, J. B., Horn, K., & Karraker, K. (2004). Delay discounting and probability discounting as related to cigarette smoking status in adults. *Behav Proc, 65*(1), 35-42. doi:10.1016/S0376-6357(03)00109-8

Rhodes, E. (2019). *Neuronal network oscillations in the control of human movement.* University of Plymouth,

Richards, J. B., Zhang, L., Mitchell, S. H., & de Wit, H. (1999). Delay or probability discounting in a model of impulsive behavior: effect of alcohol. *J Exp Anal Behav, 71*(2), 121-143. doi:10.1901/jeab.1999.71-121

Richter, M. (2013). A closer look into the multi-layer structure of motivational intensity theory. *Soc Personal Psychol Compass*, 7(1), 1-12. doi:10.1111/spc3.12007

Richter, M. (2015). Goal pursuit and energy conservation: energy investment increases with task demand but does not equal it. *Mot Emot*, 39(1), 25-33. doi:10.1007/s11031-014-9429-y

Richter, M. (2016). The moderating effect of success importance on the relationship between listening demand and listening effort. *Ear Hear*, 37 Suppl 1, 111s-117s. doi:10.1097/aud.0000000000000295

Richter, M., Baeriswyl, E., & Roets, A. (2012). Personality effects on cardiovascular reactivity: need for closure moderates the impact of task difficulty on engagement-related myocardial beta-adrenergic activity. *Psychophysiol*, 49(5), 704-707. doi:10.1111/j.1469-8986.2011.01350.x

Richter, M., Friedrich, A., & Gendolla, G. H. (2008). Task difficulty effects on cardiac activity. *Psychophysiol*, 45(5), 869-875. doi:10.1111/j.1469-8986.2008.00688.x

Richter, M., Gendolla, G. H., & Wright, R. A. (2016). Three decades of research on motivational intensity theory: what we have learned about effort and what we still don't know. In Advances in motivation science (Vol. 3, pp. 149-186): Elsevier.

Richter, A., Guitart-Masip, M., Barman, A., Libeau, C., Behnisch, G., Czerney, S., . . . Schott, B. H. (2014). Valenced action/inhibition learning in humans is modulated by a genetic variant linked to dopamine D2 receptor expression. *Front Syst Neurosci*, 8, 140. doi:10.3389/fnsys.2014.00140

Riddle, C. N., & Baker, S. N. (2006). Digit displacement, not object compliance, underlies task dependent modulations in human corticomuscular coherence. *Neuroimage, 33*(2), 618-627. doi:10.1016/j.neuroimage.2006.07.027

Rieger, M., Gauggel, S., & Burmeister, K. (2003). Inhibition of ongoing responses following frontal, nonfrontal, and basal ganglia lesions. *Neuropsychol, 17*(2), 272-282. doi:10.1037/0894-4105.17.2.272

Riekkinen Jr, P., Kuitunen, J., & Riekkinen, M. (1995). Effects of scopolamine infusions into the anterior and posterior cingulate on passive avoidance and water maze navigation. *Brain Res, 685*(1-2), 46-54. doi:10.1016/0006-8993(95)00422-M

Rihs, T. A., Michel, C. M., & Thut, G. (2007). Mechanisms of selective inhibition in visual spatial attention are indexed by alpha-band EEG synchronization. *Eur J Neurosci, 25*(2), 603-610. doi:10.1111/j.1460-9568.2007.05278.x

Riley, E. P., & Foss, J. A. (1991). The acquisition of passive avoidance, active avoidance, and spatial navigation tasks by animals prenatally exposed to cocaine. *Neurotoxicol Teratol*, 13(5), 559-564. doi:10.1016/0892-0362(91)90066-6

Rinck, M., & Becker, E. S. (2007). Approach and avoidance in fear of spiders. *J Behav Thera Exp Psychiat, 38*(2), 105-120. doi:10.1016/j.jbtep.2006.10.001

Risko, E. F., Medimorec, S., Chisholm, J., & Kingstone, A. (2014). Rotating with rotated text: a natural behavior approach to investigating cognitive offloading. *Cogn Sci, 38*(3), 537-564. doi:10.1111/cogs.12087

Roach, P. J. (2002). Glycogen and its metabolism. *Curr Molecul Med, 2*(2), 101-120. doi:10.2174/1566524024605761

Roach, B. J., & Mathalon, D. H. (2008). Event-related EEG time-frequency analysis: an overview of measures and an analysis of early gamma band phase locking in schizophrenia. *Schizophr Bull*, 34(5), 907-926. doi:10.1093/schbul/sbn093

Robbins, T. W., & Everitt, B. J. (2007). A role for mesencephalic dopamine in activation: commentary on Berridge (2006). *Psychopharmacol, 191*(3), 433-437. doi:10.1007/s00213-006-0528-7

Robinson, P. A., Krimsky, M., & Grillon, C. (2013). The impact of induced anxiety on response inhibition. *Front Hum Neurosci, 7*, 69. doi:10.3389/fnhum.2013.00069

Robinson, P. A., Rennie, C. J., Wright, J. J., Bahramali, H., Gordon, E., & Rowe, D. L. (2001). Prediction of electroencephalographic spectra from neurophysiology. *Phys Rev E Stat Nonlin Soft Matter Phys, 63*(2 Pt 1), 021903. doi:10.1103/PhysRevE.63.021903

Rodríguez-Gómez, P., Pozo, M., Hinojosa, J. A., & Moreno, E. M. (2019). Please be logical, I am in a bad mood: An electrophysiological study of mood effects on reasoning. *Neuropsychologia*, 127, 19-28. doi:10.1016/j.neuropsychologia.2019.02.008

Roesch, M. R., Taylor, A. R., & Schoenbaum, G. (2006). Encoding of time-discounted rewards in orbitofrontal cortex is independent of value representation. *Neuron, 51*(4), 509-520. doi:10.1016/j.neuron.2006.06.027

Roets, A., Van Hiel, A., Cornelis, I., & Soetens, B. (2008). Determinants of task performance and invested effort: a need for closure by relative cognitive capacity interaction analysis. *Pers Soc Psychol Bull*, 34(6), 779-792. doi:10.1177/0146167208315554

Rogers, R. D., Owen, A. M., Middleton, H. C., Williams, E. J., Pickard, J. D., Sahakian, B. J., & Robbins, T. W. (1999). Choosing between small, likely rewards and large, unlikely rewards activates inferior and orbital prefrontal

cortex. *J Neurosci, 19*(20), 9029-9038. doi:10.1523/JNEUROSCI.19-20-09029.1999

Rohenkohl, G., & Nobre, A. C. (2011). Alpha oscillations related to anticipatory attention follow temporal expectations. *J Neurosci, 31*(40), 14076-14084. doi:10.1523/JNEUROSCI.3387-11.2011

Romei, V., Brodbeck, V., Michel, C., Amedi, A., Pascual-Leone, A., & Thut, G. (2008). Spontaneous fluctuations in posterior alpha-band EEG activity reflect variability in excitability of human visual areas. *Cereb Cortex, 18*(9), 2010-2018. doi:10.1093/cercor/bhm229

Romei, V., Gross, J., & Thut, G. (2010). On the role of prestimulus alpha rhythms over occipito-parietal areas in visual input regulation: correlation or causation? *J Neurosci, 30*(25), 8692-8697. doi:10.1523/jneurosci.0160-10.2010

Rondeel, E. W., van Steenbergen, H., Holland, R. W., & van Knippenberg, A. (2015). A closer look at cognitive control: differences in resource allocation during updating, inhibition and switching as revealed by pupillometry. Front Hum Neurosci, 9, 494. doi:10.3389/fnhum.2015.00494

Rönnberg, J., Lunner, T., Zekveld, A., Sörqvist, P., Danielsson, H., Lyxell, B., . . . Rudner, M. (2013). The Ease of Language Understanding (ELU) model: theoretical, empirical, and clinical advances. Front Syst Neurosci, 7, 31. doi:10.3389/fnsys.2013.00031

Rönnberg, J., Rudner, M., Foo, C., & Lunner, T. (2008). Cognition counts: a working memory system for ease of language understanding (ELU). Int J Audiol, 47 Suppl 2, S99-105. doi:10.1080/14992020802301167

Roopun, A. K., Middleton, S. J., Cunningham, M. O., LeBeau, F. E., Bibbig, A., Whittington, M. A., & Traub, R. D. (2006). A beta2-frequency (20-30 Hz) oscillation in nonsynaptic networks of somatosensory cortex. *Proc Natl Acad Sci 103*(42), 15646-15650. doi:10.1073/pnas.0607443103

Rosenbaum, D. A., & Gaydos, M. J. (2008). A method for obtaining psychophysical estimates of movement costs. *J Motor Behav, 40*(1), 11-17. doi:10.3200/JMBR.40.1.11-17

Rossiter, H. E., Davis, E. M., Clark, E. V., Boudrias, M. H., & Ward, N. S. (2014). Beta oscillations reflect changes in motor cortex inhibition in healthy ageing. *Neuroimage, 91*(100), 360-365. doi:10.1016/j.neuroimage.2014.01.012

Rosso, A. L., Studenski, S. A., Chen, W. G., Aizenstein, H. J., Alexander, N. B., Bennett, D. A., . . . Rosano, C. (2013). Aging, the central nervous system, and mobility. *J Gerontol A Biol Sci Med Sci*, 68(11), 1379-1386. doi:10.1093/gerona/glt089

Rothwell, J. C., Colebatch, J. G., Britton, T. C., Priori, A., Thompson, P. D., Day, B. L., & Marsden, C. D. (1991). Physiological-studies in a patient with mirror movements and agenesis of the corpus-callosum. *J PHYSIOL-LONDON, 438*, P34-P34. doi:2434/193544

Rougeul, A., Bouyer, J. J., Dedet, L., & Debray, O. (1979). Fast somato-parietal rhythms during combined focal attention and immobility in baboon and squirrel monkey. *Electroencephalogr Clin Neurophysiol, 46*(3), 310-319. doi:10.1016/0013-4694(79)90205-0

Rozin, P., & Royzman, E. B. (2001). Negativity bias, negativity dominance, and contagion. *Personal Soc Psychol Rev, 5*(4), 296-320. doi:10.1207/S15327957PSPR0504_2

Rubia, K., Taylor, E., Smith, A. B., Oksanen, H., Overmeyer, S., & Newman, S. (2001). Neuropsychological analyses of impulsiveness in childhood hyperactivity. *Br J Psychiatry, 179*, 138-143. doi:10.1192/bjp.179.2.138

Ruchala, L. V. (1999). The influence of budget goal attainment on risk attitudes and escalation. *Behav Res Account, 11*, 161. doi:7fbac7b9c310bc032c22fd3c887000ac

Russ, D. W., Elliott, M. A., Vandenborne, K., Walter, G. A., & Binder-Macleod, S. A. (2002). Metabolic costs of isometric force generation and maintenance of human skeletal muscle. *Am J Physiol Endocrinol Metab*, 282(2), E448-457. doi:10.1152/ajpendo.00285.2001

Russell, J. A. (2003). Core affect and the psychological construction of emotion. *Psychol Rev, 110*(1), 145-172. doi:10.1037/0033-295x.110.1.145

Rutishauser, U., Ross, I. B., Mamelak, A. N., & Schuman, E. M. (2010). Human memory strength is predicted by theta-frequency phase-locking of single neurons. *Nature, 464*(7290), 903-907. doi:10.1038/nature08860

Sailer, A., Dichgans, J., & Gerloff, C. (2000). The influence of normal aging on the cortical processing of a simple motor task. *Neurology*, 55(7), 979-985. doi:10.1212/wnl.55.7.979

Sakamak, I., Tavakoli, M., Wiebe, S., & Adams, K. (2020). Integration of an eye gaze interface and BCI with biofeedback for human-robot *Interaction*. doi:10.7939/r3-n8hm-0p20

Sakagami, M., Pan, X., & Uttl, B. (2006). Behavioral inhibition and prefrontal cortex in decision-making. *Neural Netw, 19*(8), 1255-1265. doi:10.1016/j.neunet.2006.05.040

Salamone, J. D. (1994). The involvement of nucleus accumbens dopamine in appetitive and aversive motivation. *Behav Brain Res*, 61(2), 117-133. doi:10.1016/0166-4328(94)90153-8

Salamone, J. D. (2009). Dopamine, effort, and decision making: theoretical comment on Bardgett et al. (2009). *Behav Neurosci, 123*(2), 463-467. doi:10.1037/a0015381

Salamone, J. D., Correa, M., Farrar, A., & Mingote, S. M. (2007). Effort-related functions of nucleus accumbens dopamine and associated forebrain circuits. *Psychopharmacol, 191*(3), 461-482. doi:10.1007/s00213-006-0668-9

Salamone, J. D., Correa, M., Mingote, S., & Weber, S. M. (2003). Nucleus accumbens dopamine and the regulation of effort in food-seeking behavior: implications for studies of natural motivation, psychiatry, and drug abuse. *J Pharmacol Exp Ther, 305*(1), 1-8. doi:10.1124/jpet.102.035063

Salamone, J. D., Cousins, M. S., & Snyder, B. J. (1997). Behavioral functions of nucleus accumbens dopamine: empirical and conceptual problems with the anhedonia hypothesis. *Neurosci Biobehav Rev, 21*(3), 341-359. doi:10.1016/S0149-7634(96)00017-6

Salamone, J. D., Steinpreis, R. E., McCullough, L. D., Smith, P., Grebel, D., & Mahan, K. (1991). Haloperidol and nucleus accumbens dopamine depletion suppress lever pressing for food but increase free food consumption in a novel food choice procedure. *Psychopharmacol, 104*(4), 515-521. doi:10.1007/bf02245659

Salamone, J. D., Wisniecki, A., Carlson, B. B., & Correa, M. (2001). Nucleus accumbens dopamine depletions make animals highly sensitive to high fixed

ratio requirements but do not impair primary food reinforcement. *Neurosci, 105*(4), 863-870. doi:10.1016/s0306-4522(01)00249-4

Salinas, E., & Sejnowski, T. J. (2001). Correlated neuronal activity and the flow of neural information. *Nat Rev Neurosci, 2*(8), 539-550. doi:10.1038/35086012

Salmelin, R., Hamalainen, M., Kajola, M., & Hari, R. (1995). Functional segregation of movement-related rhythmic activity in the human brain. *Neuroimage, 2*(4), 237-243. doi:10.1006/nimg.1995.1031

Salmelin, R., & Hari, R. (1994). Spatiotemporal characteristics of sensorimotor neuromagnetic rhythms related to thumb movement. *Neurosci, 60*(2), 537-550. doi:0306-4522(94)E0020-5

Salzman, C. D., Paton, J. J., Belova, M. A., & Morrison, S. E. (2007). Flexible neural representations of value in the primate brain. *Ann N Y Acad Sci*, 1121, 336-354. doi:10.1196/annals.1401.034

Samar, V. J., Bopardikar, A., Rao, R., & Swartz, K. (1999). Wavelet analysis of neuroelectric waveforms: a conceptual tutorial. *Brain Lang*, 66(1), 7-60. doi:10.1006/brln.1998.2024

Samkoff, J. S., & Jacques, C. H. (1991). A review of studies concerning effects of sleep deprivation and fatigue on residents' performance. *Acad Med*. doi:10.1097/00001888-199111000-00013

Sanes, J. N., & Donoghue, J. P. (1993). Oscillations in local field potentials of the primate motor cortex during voluntary movement. *Proc Natl Acad Sci, 90*(10), 4470-4474. doi:10.1073/pnas.90.10.4470

Sassenhagen, J., & Draschkow, D. (2019). Cluster-based permutation tests of MEG/EEG data do not establish significance of effect latency or location. *Psychophysiol*, 56(6), e13335. doi:10.1111/psyp.13335

Satterthwaite, T. D., Green, L., Myerson, J., Parker, J., Ramaratnam, M., & Buckner, R. L. (2007). Dissociable but inter-related systems of cognitive control and reward during decision making: evidence from pupillometry and event-related fMRI. *Neuroimage, 37*(3), 1017-1031. doi:10.1016/j.neuroimage.2007.04.066

Scerbo, M. W. (2001). Stress, workload, and boredom in vigilance: a problem and an answer. *Stress Workload Fatigue*.

Schacter, D. L. (1977). EEG theta waves and psychological phenomena: a review and analysis. *Biol Psychol,* 5(1), 47-82. doi:10.1016/0301-0511(77)90028-x

Scheres, A., Dijkstra, M., Ainslie, E., Balkan, J., Reynolds, B., Sonuga-Barke, E., & Castellanos, F. X. (2006). Temporal and probabilistic discounting of rewards in children and adolescents: effects of age and ADHD symptoms. *Neuropsychol, 44*(11), 2092-2103. doi:10.1016/j.neuropsychologia.2005.10.012

Schevernels, H., Bombeke, K., Krebs, R. M., & Boehler, C. N. (2016). Preparing for (valenced) action: the role of differential effort in the orthogonalized Go/No-Go task. *Psychophysiol*, 53(2), 186-197. doi:10.1111/psyp.12558

Schmidt, L., Lebreton, M., Clery-Melin, M. L., Daunizeau, J., & Pessiglione, M. (2012). Neural mechanisms underlying motivation of mental versus physical effort. *PLoS Biol, 10*(2), e1001266. doi:10.1371/journal.pbio.1001266

Schneider, W., & Shiffrin, R. M. (1977). Controlled and automatic human information processing: i. detection, search, and attention. *Psychol Rev, 84*(1), 1. doi:10.1037/0033-295X.84.1.1

Schneider, W., & Strüder, H. K. (2012). EEG: theoretical background and practical aspects. In *Functional neuroimaging in exercise and sport sciences* (pp. 197-212). New York, United States: Springer.

Schneirla, T. C. (1959). An evolutionary and developmental theory of biphasic processes underlying approach and withdrawal. *Nebraska Sympos Mot*.

Schnitzler, A., Salenius, S., Salmelin, R., Jousmaki, V., & Hari, R. (1997). Involvement of primary motor cortex in motor imagery: a neuromagnetic study. *Neuroimage, 6*(3), 201-208. doi:10.1006/nimg.1997.0286

Schoffelen, J. M., Oostenveld, R., & Fries, P. (2008). Imaging the human motor system's beta-band synchronization during isometric contraction. *Neuroimage, 41*(2), 437-447. doi:10.1016/j.neuroimage.2008.01.045

Schreckenberger, M., Lange-Asschenfeldt, C., Lochmann, M., Mann, K., Siessmeier, T., Buchholz, H. G., . . . Gründer, G. (2004). The thalamus as the generator and modulator of EEG alpha rhythm: a combined PET/EEG study with lorazepam challenge in humans. *Neuroimage, 22*(2), 637-644. doi:10.1016/j.neuroimage.2004.01.047

Schultz, W. (2015). Neuronal reward and decision signals: from theories to data. *Physiol Rev, 95*(3), 853-951. doi:10.1152/physrev.00023.2014

Schultz, W., Tremblay, L., & Hollerman, J. R. (2000). Reward processing in primate orbitofrontal cortex and basal ganglia. *Cereb Cortex*, 10(3), 272-284. doi:10.1093/cercor/10.3.272

Schutzwohl, A. (2018). Approach and avoidance during routine behavior and during surprise in a non-evaluative task: surprise matters and so does the valence of the surprising event. *Front Psychol, 9*, 826. doi:10.3389/fpsyg.2018.00826

Scott, S. H. (2012). The computational and neural basis of voluntary motor control and planning. *Trends Cogn Sci, 16*(11), 541-549. doi:10.1016/j.tics.2012.09.008

Seaman, K. L., Brooks, N., Karrer, T. M., Castrellon, J. J., Perkins, S. F., Dang, L. C., . . . Samanez-Larkin, G. R. (2018). Subjective value representations during effort, probability and time discounting across adulthood. *Soc Cogn Affect Neurosci, 13*(5), 449-459. doi:10.1093/scan/nsy021

Segers, P., Steendijk, P., Stergiopulos, N., & Westerhof, N. (2001). Predicting systolic and diastolic aortic blood pressure and stroke volume in the intact sheep. *J Biomech,* 34(1), 41-50. doi:10.1016/s0021-9290(00)00165-2

Seidler, R. D., Bernard, J. A., Burutolu, T. B., Fling, B. W., Gordon, M. T., Gwin, J. T., . . . Lipps, D. B. (2010). Motor control and aging: links to age-related brain structural, functional, and biochemical effects. *Neurosci Biobehav Rev,* 34(5), 721-733. doi:10.1016/j.neubiorev.2009.10.005

Seifert, J., Naumann, E., Hewig, J., Hagemann, D., & Bartussek, D. (2006). Motivated executive attention--incentives and the noise-compatibility effect. *Biol Psychol, 71*(1), 80-89. doi:10.1016/j.biopsycho.2005.03.001

Serences, J. T., & Yantis, S. (2006). Selective visual attention and perceptual coherence. *Trends Cogn Sci, 10*(1), 38-45. doi:10.1016/j.tics.2005.11.008

Sergeant, J., Geuze, R., & Van Winsum, W. (1987). Event-related desynchronization and P300. *Psychophysiol, 24*(3), 272-277. doi: 10.1111/j.1469-8986.1987.tb00294.x

Sestieri, C., Sylvester, C. M., Jack, A. I., d'Avossa, G., Shulman, G. L., & Corbetta, M. (2008). Independence of anticipatory signals for spatial attention from

number of nontarget stimuli in the visual field. *J Neurophysiol, 100*(2), 829-838. doi:10.1152/jn.00030.2008

Shallice, T. (1994). Multiple levels of control processes. *Atten Perfor*, 395-420.

Sharp, M. E., Foerde, K., Daw, N. D., & Shohamy, D. (2016). Dopamine selectively remediates 'model-based' reward learning: a computational approach. *Brain, 139*(Pt 2), 355-364. doi:10.1093/brain/awv347

Shenhav, A., Botvinick, M. M., & Cohen, J. D. (2013a). The expected value of control: an integrative theory of anterior cingulate cortex function. *Neuron, 79*(2), 217-240. doi:10.1016/j.neuron.2013.07.007

Shenhav, A., Botvinick, M. M., & Cohen, J. D. (2013b). The expected value of control: an integrative theory of anterior cingulate cortex function. *Neuron, 79*(2), 217-240. doi:10.1016/j.neuron.2013.07.007

Shenhav, A., Musslick, S., Lieder, F., Kool, W., Griffiths, T. L., Cohen, J. D., & Botvinick, M. M. (2017). Toward a rational and mechanistic account of mental effort. *Ann Rev Neurosci, 40*, 99-124. doi:10.1146/annurev-neuro-072116-031526

Shibasaki, H., & Hallett, M. (2006). What is the Bereitschaftspotential? *Clin neurophysiol*, 117(11), 2341-2356.

Shimazu, H., Kaji, R., Murase, N., Kohara, N., Ikeda, A., Shibasaki, H., . . . Rothwell, J. C. (1999). Pre-movement gating of short-latency somatosensory evoked potentials. *Neuroreport, 10*(12), 2457-2460. doi:10.1097/00001756-199908200-00004

Shohamy, D., & Adcock, R. A. (2010). Dopamine and adaptive memory. *Trends Cogn Sci, 14*(10), 464-472. doi:10.1016/j.tics.2010.08.002

Shoji, M., Golde, T. E., Ghiso, J., Cheung, T. T., Estus, S., Shaffer, L. M., . . . Frangione, B. (1992). Production of the Alzheimer amyloid beta protein by normal proteolytic processing. *Sci, 258*(5079), 126-129. doi:10.1126/science.1439760

Siegle, G. J., Ichikawa, N., & Steinhauer, S. (2008). Blink before and after you think: blinks occur prior to and following cognitive load indexed by pupillary responses. *Psychophysiol*, 45(5), 679-687. doi:10.1111/j.1469-8986.2008.00681.x

Siegle, G. J., Steinhauer, S. R., & Thase, M. E. (2004). Pupillary assessment and computational modeling of the Stroop task in depression. *Int J Psychophysiol*, 52(1), 63-76. doi:10.1016/j.ijpsycho.2003.12.010

Siegel, M., Donner, T. H., Oostenveld, R., Fries, P., & Engel, A. K. (2007). High-frequency activity in human visual cortex is modulated by visual motion strength. *Cereb Cortex, 17*(3), 732-741. doi:10.1093/cercor/bhk025

Siegel, M., Donner, T. H., Oostenveld, R., Fries, P., & Engel, A. K. (2008). Neuronal synchronization along the dorsal visual pathway reflects the focus of spatial attention. *Neuron, 60*(4), 709-719. doi:10.1016/j.neuron.2008.09.010

Simmonds, D. J., Pekar, J. J., & Mostofsky, S. H. (2008). Meta-analysis of Go/No-go tasks demonstrating that fMRI activation associated with response inhibition is task-dependent. *Neuropsychologia, 46*(1), 224-232.

Singer, W. (1993). Synchronization of cortical activity and its putative role in information processing and learning. *Annu Rev Physiol, 55*, 349-374. doi:10.1146/annurev.ph.55.030193.002025

Singh, K. D., Barnes, G. R., Hillebrand, A., Forde, E. M., & Williams, A. L. (2002). Task-related changes in cortical synchronization are spatially coincident with

the hemodynamic response. *Neuroimage, 16*(1), 103-114. doi:10.1006/nimg.2001.1050

Sinha, N., Manohar, S., & Husain, M. (2013). Impulsivity and apathy in Parkinson's disease. *J Neuropsychol, 7*(2), 255-283. doi:10.1111/jnp.12013

Skulmowski, A., & Rey, G. D. (2017). Bodily Effort Enhances Learning and Metacognition: Investigating the Relation Between Physical Effort and Cognition Using Dual-Process Models of Embodiment. *Adv Cogn Psychol*, 13(1), 3-10. doi:10.5709/acp-0202-9

Sloman, S. A. (1996). The empirical case for two aystems of reasoning. *Psychol Bull, 119*(1), 3. doi:10.1037/0033-2909.119.1.3

Small, D. M., Gitelman, D., Simmons, K., Bloise, S. M., Parrish, T., & Mesulam, M. M. (2005). Monetary incentives enhance processing in brain regions mediating top-down control of attention. *Cereb Cortex, 15*(12), 1855-1865. doi:10.1093/cercor/bhi063

Smit, A. S., Eling, P. A., & Coenen, A. M. (2004). Mental effort affects vigilance enduringly: after-effects in EEG and behavior. *Int J Psychophysiol*, 53(3), 239-243. doi:10.1016/j.ijpsycho.2004.04.005

Smith, K. R., Lawyer, S. R., & Swift, J. K. (2018). A meta-analysis of nonsystematic responding in delay and probability reward discounting. *Exp Clin Psychopharmacol, 26*(1), 94-107. doi:10.1037/pha0000167

Snyder, A. C., & Foxe, J. J. (2010). Anticipatory attentional suppression of visual features indexed by oscillatory alpha-band power increases: a high-density electrical mapping study. *J Neurosci, 30*(11), 4024-4032. doi:10.1523/jneurosci.5684-09.2010

Sohn, Y. H., Wiltz, K., & Hallett, M. (2002). Effect of volitional inhibition on cortical inhibitory mechanisms. *J Neurophysiol*, 88(1), 333-338. doi:10.1152/jn.2002.88.1.333

Sokol-Hessner, P., Camerer, C. F., & Phelps, E. A. (2013). Emotion regulation reduces loss aversion and decreases amygdala responses to losses. *Soc Cog Affect Neurosci, 8*(3), 341-350. doi:10.1093/scan/nss002

Sokol-Hessner, P., Hsu, M., Curley, N. G., Delgado, M. R., Camerer, C. F., & Phelps, E. A. (2009). Thinking like a trader selectively reduces individuals' loss aversion. *Proc Natl Acad Sci*, 106(13), 5035-5040. doi:10.1073/pnas.0806761106

Solarz, A. K. (1960). Latency of instrumental responses as a function of compatibility with the meaning of eliciting verbal signs. *J Exp Psychol, 59*, 239-245. doi:10.1037/h0047274

Solis-Escalante, T., Muller-Putz, G. R., Pfurtscheller, G., & Neuper, C. (2012). Cue-induced beta rebound during withholding of overt and covert foot movement. *Clin Neurophysiol, 123*(6), 1182-1190. doi:10.1016/j.clinph.2012.01.013

Sommer, M., Classen, J., Cohen, L. G., & Hallett, M. (2001). Time course of determination of movement direction in the reaction time task in humans. J *Neurophysiol*, 86(3), 1195-1201. doi:10.1152/jn.2001.86.3.1195

Soutschek, A., Kang, P., Ruff, C. C., Hare, T. A., & Tobler, P. N. (2018). Brain stimulation over the frontopolar cortex enhances motivation to exert effort for reward. *Biol Psychiatr*, 84(1), 38-45. doi:10.1016/j.biopsych.2017.11.007

Spaak, E., de Lange, F. P., & Jensen, O. (2014). Local entrainment of alpha oscillations by visual stimuli causes cyclic modulation of perception. *J Neurosci, 34*(10), 3536-3544. doi:10.1523/jneurosci.4385-13.2014

Speckmann, E., Elger, C., & Gorji, A. (2011). Neurophysiologic basis of EEG and DC potentials. *Electroencephalography: Basic Principles, Clinical Applications and Related Fields, Lippincott Williams & Wilkins, Philadelphia*, 17-32.

Spinks, R. L., Kraskov, A., Brochier, T., Umilta, M. A., & Lemon, R. N. (2008). Selectivity for grasp in local field potential and single neuron activity recorded simultaneously from M1 and F5 in the awake macaque monkey. *J Neurosci, 28*(43), 10961-10971. doi:10.1523/jneurosci.1956-08.2008

Spires-Jones, T. L., & Hyman, B. T. (2014). The Intersection of amyloid beta and tau at synapses in Alzheimer's disease. *Neuron, 82*(4), 756-771. doi:10.1016/j.neuron.2014.05.004

Sprinkle, G. B., Williamson, M. G., & Upton, D. R. (2008). The effort and risk-taking effects of budget-based contracts. *Account Org Soc, 33*(4-5), 436-452. doi:10.1016/j.aos.2007.11.001

Stancak, A., Jr., Feige, B., Lucking, C. H., & Kristeva-Feige, R. (2000). Oscillatory cortical activity and movement-related potentials in proximal and distal movements. *Clin Neurophysiol, 111*(4), 636-650.

Stancak, A., Jr., & Pfurtscheller, G. (1996). Mu-rhythm changes in brisk and slow self-paced finger movements. *Neuroreport, 7*(6), 1161-1164. doi:10.1097/00001756-199604260-00013

Stancak, A., & Pfurtscheller, G. (1995). Desynchronization and recovery of beta rhythms during brisk and slow self-paced finger movements in man. *Neurosci Lett, 196*(1-2), 21-24. doi:10.1016/0304-3940(95)11827-j

Stancak, A., & Pfurtscheller, G. (1996). Event-related desynchronisation of central beta-rhythms during brisk and slow self-paced finger movements of dominant

and nondominant hand. *Brain Res Cogn Brain Res, 4*(3), 171-183. doi:10.1016/S0926-6410(96)00031-6

Stancak, A., Riml, A., & Pfurtscheller, G. (1997). The effects of external load on movement-related changes of the sensorimotor EEG rhythms. *Electroencephalogr Clin Neurophysiol, 102*(6), 495-504. doi:10.1016/S0013-4694(96)96623-0

Stancak, A., Xie, Y., Fallon, N., Bulsing, P., Giesbrecht, T., Thomas, A., & Pantelous, A. A. (2015). Unpleasant odors increase aversion to monetary losses. *Bio Psychol*, 107, 1-9. doi:10.1016/j.biopsycho.2015.02.006

Stanek, J., C., & Richter, M. (2021). Energy investment and motivation: The additive impact of task demand and reward value on exerted force in hand grip tasks. *Mot Emot*, 1-15. doi:10.1007/s11031-020-09862-2

Stedman, A., Davey, N. J., & Ellaway, P. H. (1998). Facilitation of human first dorsal interosseous muscle responses to transcranial magnetic stimulation during voluntary contraction of the contralateral homonymous muscle. *Muscle Nerve, 21*(8), 1033-1039.

Steenkamp, J. E., & Baumgartner, H. (1992). The role of optimum stimulation level in exploratory consumer behavior. *J Cons Res, 19*(3), 434-448. doi:10.1086/209313

Stefanics, G., Hangya, B., Hernadi, I., Winkler, I., Lakatos, P., & Ulbert, I. (2010). Phase entrainment of human delta oscillations can mediate the effects of expectation on reaction speed. *J Neurosci, 30*(41), 13578-13585. doi:10.1523/jneurosci.0703-10.2010

Steriade, M. (1999). Coherent oscillations and short-term plasticity in corticothalamic networks. *Trends Neurosci, 22*(8), 337-345. doi:10.1016/s0166-2236(99)01407-1

Steriade, M. (2000). Corticothalamic resonance, states of vigilance and mentation. *Neurosci, 101*(2), 243-276. doi:10.1016/S0306-4522(00)00353-5

Steriade, M., & Demetrescu, M. (1962). Reticular facilitation of responses to acoustic stimuli. *Electroencephalogr Clin Neurophysiol, 14*, 21-36.

Sterman, M. B., Kaiser, D. A., & Veigel, B. (1996). Spectral analysis of event-related EEG responses during short-term memory performance. *Brain Topo, 9*(1), 21-30. doi:10.1007/BF01191639

Stevenson, C. M., Brookes, M. J., & Morris, P. G. (2011). β-Band correlates of the fMRI BOLD response. *Hum Brain Mapp, 32*(2), 182-197. doi:10.1002/hbm.21016

Stinear, C. M., Coxon, J. P., & Byblow, W. D. (2009). Primary motor cortex and movement prevention: where Stop meets Go. *Neurosci Biobehav Rev, 33*(5), 662-673. doi:10.1016/j.neubiorev.2008.08.013

Stinear, C. M., Walker, K. S., & Byblow, W. D. (2001). Symmetric facilitation between motor cortices during contraction of ipsilateral hand muscles. *Exp Brain Res, 139*(1), 101-105. doi:10.1007/s002210100758

Stuss, D. T., & Benson, D. F. (1984). Neuropsychological studies of the frontal lobes. *Psychol Bull, 95*(1), 3-28. doi:10.1037/0033-2909.95.1.3

Suffczynski, P. (1999). Event-Related Dynamics of alpha band rhythms: a neuronal network model of focal ERD/surround ERS. *Handbook Electroencephal Clin Neurophysiol, 6*, 67-85.

Suffczynski, P., Kalitzin, S., Pfurtscheller, G., & Da Silva, F. L. (2001). Computational model of thalamo-cortical networks: dynamical control of alpha rhythms in relation to focal attention. *Int J Psychophysiol, 43*(1), 25-40.

Sugiwaka, H., & Okouchi, H. (2004). Reformative self-control and discounting of reward value by delay or effort. *Psychol Res, 46*(1), 1-9. doi:10.1111/j.1468-5884.2004.00231.x

Sugrue, L. P., Corrado, G. S., & Newsome, W. T. (2004). Matching behavior and the representation of value in the parietal cortex. *Sci, 304*(5678), 1782-1787. doi:10.1126/science.1094765

Swann, N., Tandon, N., Canolty, R., Ellmore, T. M., McEvoy, L. K., Dreyer, S., . . . Aron, A. R. (2009). Intracranial EEG Reveals a time- and frequency-specific role for the right inferior frontal gyrus and primary motor cortex in stopping initiated responses. *J Neurosci, 29*(40), 12675-12685. doi:10.1523/jneurosci.3359-09.2009

Swick, D., Ashley, V., & Turken, U. (2011). Are the neural correlates of stopping and not going identical? Quantitative meta-analysis of two response inhibition tasks. *Neuroimage, 56*(3), 1655-1665. doi:10.1016/j.neuroimage.2011.02.070

Sylvester, C. M., Jack, A. I., Corbetta, M., & Shulman, G. L. (2008). Anticipatory suppression of nonattended locations in visual cortex marks target location and predicts perception. *J Neurosci, 28*(26), 6549-6556. doi:10.1523/jneurosci.0275-08.2008

Sylvester, C. M., Shulman, G. L., Jack, A. I., & Corbetta, M. (2007). Asymmetry of anticipatory activity in visual cortex predicts the locus of attention and

perception. *J Neurosci, 27*(52), 14424-14433. doi:10.1523/jneurosci.3759-07.2007

Szentesi, P., Zaremba, R., van Mechelen, W., & Stienen, G. J. (2001). ATP utilization for calcium uptake and force production in different types of human skeletal muscle fibres. *J Physiol*, 531(Pt 2), 393-403. doi:10.1111/j.1469-7793.2001.0393i.x

Talelli, P., Ewas, A., Waddingham, W., Rothwell, J. C., & Ward, N. S. (2008). Neural correlates of age-related changes in cortical neurophysiology. Neuroimage, 40(4), 1772-1781. doi:10.1016/j.neuroimage.2008.01.039

Talmi, D., Dayan, P., Kiebel, S. J., Frith, C. D., & Dolan, R. J. (2009). How humans integrate the prospects of pain and reward during choice. *J Neurosci*, 29(46), 14617-14626. doi:10.1523/jneurosci.2026-09.2009

Tang, D., Hu, L., & Chen, A. (2013). The neural oscillations of conflict adaptation in the human frontal region. *Biol Psychol, 93*(3), 364-372. doi:10.1016/j.biopsycho.201

Taniwaki, T., Okayama, A., Yoshiura, T., Togao, O., Nakamura, Y., Yamasaki, T., . . . Tobimatsu, S. (2007). Age-related alterations of the functional interactions within the basal ganglia and cerebellar motor loops in vivo. *Neuroimage,* 36(4), 1263-1276. doi:10.1016/j.neuroimage.2007.04.027

Theorell, T., & Karasek, R. A. (1996). Current issues relating to psychosocial job strain and cardiovascular disease research. *J Occup Health Psychol,* 1(1), 9-26. doi:10.1037//1076-8998.1.1.9

Tom, S. M., Fox, C. R., Trepel, C., & Poldrack, R. A. (2007). The neural basis of loss aversion in decision-making under risk. *Sci,* 315(5811), 515-518. doi:10.1126/science.11342393.03.004

Toma, K., Matsuoka, T., Immisch, I., Mima, T., Waldvogel, D., Koshy, B., . . . Hallett, M. (2002). Generators of movement-related cortical potentials: fMRI-constrained EEG dipole source analysis. *Neuroimage, 17*(1), 161-173. doi:10.1006/nimg.2002.1165

Tatti, E., Ricci, S., Mehraram, R., Lin, N., George, S., Nelson, A. B., & Ghilardi, M. F. (2019). Beta modulation depth is not linked to movement features. *Front Behav Neurosci, 13*, 49. doi:10.3389/fnbeh.2019.00049

Taylor, S. E. (1991). Asymmetrical effects of positive and negative events: the mobilization-minimization hypothesis. *Psychol Bull, 110*(1), 67-85. doi:10.1037/0033-2909.110.1.67

Teplan, M. (2002). Fundamentals of EEG measurement. *Measure Sci Rev, 2*(2), 1-11.

Terrell, H. K., Derenne, A., & Weatherly, J. N. (2014). Exploratory and confirmatory factor analyses of probability discounting of different outcomes across different methods of measurement. *Ann J Psychol, 127*(2), 215-231. doi:10.5406/amerjpsyc.127.2.0215

Tewarie, P., Hunt, B. A. E., O'Neill, G. C., Byrne, A., Aquino, K., Bauer, M., . . . Brookes, M. J. (2018). Relationships between neuronal oscillatory amplitude and dynamic functional connectivity. *Cereb Cortex*. doi:10.1093/cercor/bhy136

Thaler, R. H. (1981). Some empirical evidence on dynamic inconsistency. *Econ Lett, 8*(3), 201-207. doi:10.1016/0165-1765(81)90067-7

Thut, G., Nietzel, A., Brandt, S. A., & Pascual-Leone, A. (2006). Alpha-band electroencephalographic activity over occipital cortex indexes visuospatial

attention bias and predicts visual target detection. *J Neurosci, 26*(37), 9494-9502. doi:10.1523/jneurosci.0875-06.2006

Thut, G., Nietzel, A., & Pascual-Leone, A. (2005). Dorsal posterior parietal rTMS affects voluntary orienting of visuospatial attention. *Cereb Cortex, 15*(5), 628-638. doi:10.1093/cercor/bhh164

Tinazzi, M., & Zanette, G. (1998). Modulation of ipsilateral motor cortex in man during unimanual finger movements of different complexities. *Neurosci Lett, 244*(3), 121-124. doi:10.1016/S0304-3940(98)00150-5

Tobler, P. N., O'Doherty, J. P., Dolan, R. J., & Schultz, W. (2007). Reward value coding distinct from risk attitude-related uncertainty coding in human reward systems. *J Neurophysiol, 97*(2), 1621-1632. doi:10.1152/jn.00745.2006

Tom, S. M., Fox, C. R., Trepel, C., & Poldrack, R. A. (2007). The neural basis of loss aversion in decision-making under risk. *Sci, 315*(5811), 515-518. doi:10.1126/science.1134239

Tombini, M., Zappasodi, F., Zollo, L., Pellegrino, G., Cavallo, G., Tecchio, F., . . . Rossini, P. M. (2009). Brain activity preceding a 2D manual catching task. *Neuroimage, 47*(4), 1735-1746. doi:10.1016/j.neuroimage.2009.04.046

Tooby, J., & Cosmides, L. (2008). The evolutionary psychology of the emotions and their relationship to internal regulatory variables. *Handbook Emot*, 114–137.

Toro, C., Deuschl, G., Thatcher, R., Sato, S., Kufta, C., & Hallett, M. (1994). Event-related desynchronization and movement-related cortical potentials on the ECoG and EEG. *Electroencephalogr Clin Neurophysiol, 93*(5), 380-389. doi:10.1016/0168-5597(94)90126-0

Tran, T., Hagen, A. E., Hollenstein, T., & Bowie, C. R. (2020). Physical-and Cognitive-Effort-Based Decision-Making in Depression: Relationships to

Symptoms and Functioning. *Clin Psychol Sci*, 2167702620949236. doi:10.1177/2167702620949236

Tran, Y., Craig, A., Bartrop, R., & Nicholson, G. (2004). Time course and regional distribution of cortical changes during acute alcohol ingestion. *Int J Neurosci, 114*(7), 863-878. doi:10.1080/00207450490450055

Treadway, M. T., Bossaller, N. A., Shelton, R. C., & Zald, D. H. (2012). Effort-based decision-making in major depressive disorder: a translational model of motivational anhedonia. *J Abnormal Psychol, 121*(3), 553. doi:10.1037/a0028813

Tritsch, N. X., Granger, A. J., & Sabatini, B. L. (2016). Mechanisms and functions of GABA co-release. *Nature Rev Neurosci, 17*(3), 139.

Tsujimoto, T., Shimazu, H., Isomura, Y., & Sasaki, K. (2010). Theta oscillations in primate prefrontal and anterior cingulate cortices in forewarned reaction time tasks. *J Neurophysiol, 103*(2), 827-843. doi:10.1152/jn.00358.2009

Tversky, A., & Kahneman, D. (1991). Loss aversion in riskless choice: a reference-dependent model. *J Econ, 106*(4), 1039-1061. doi:10.2307/2937956

Tversky, A., & Kahneman, D. (1992). Advances in prospect theory: cumulative representation of uncertainty. *J Risk Uncertainty, 5*(4), 297-323. doi:10.1007/BF00122574

Tzagarakis, C., Ince, N. F., Leuthold, A. C., & Pellizzer, G. (2010). Beta-band activity during motor planning reflects response uncertainty. *J Neurosci, 30*(34), 11270-11277. doi:10.1523/JNEUROSCI.6026-09.2010

Tzagarakis, C., West, S., & Pellizzer, G. (2015). Brain oscillatory activity during motor preparation: effect of directional uncertainty on beta, but not alpha, frequency band. *Front Neurosci, 9*, 246. doi:10.3389/fnins.2015.00246

Uebel, H., Albrecht, B., Asherson, P., Börger, N. A., Butler, L., Chen, W., . . . Banaschewski, T. (2010). Performance variability, impulsivity errors and the impact of incentives as gender-independent endophenotypes for ADHD. *J Child Psychol Psychiatry, 51*(2), 210-218. doi:10.1111/j.1469-7610.2009.02139.x

Umemoto, A., Inzlicht, M., & Holroyd, C. B. (2019). Electrophysiological indices of anterior cingulate cortex function reveal changing levels of cognitive effort and reward valuation that sustain task performance. Neuropsychologia, 123, 67-76. doi:10.1016/j.neuropsychologia.2018.06.010

Umemoto, A., & Holroyd, C. B. (2015). Task-specific effects of reward on task switching. *Psychol Res*, 79(4), 698-707. doi:10.1007/s00426-014-0595-z

Urata, J., Uchiyama, M., Iyo, M., Enomoto, T., Hayakawa, T., Tomiyama, M., . . . Okawa, M. (1996). Effects of a small dose of triazolam on P300 and resting EEG. *Psychopharmacol, 125*(2), 179-184. doi:10.1007/bf02249418

Vaish, A., Grossmann, T., & Woodward, A. (2008). Not all emotions are created equal: the negativity bias in social-emotional development. *Psychol Bull, 134*(3), 383-403. doi:10.1037/0033-2909.134.3.383

Vallesi, A., McIntosh, A. R., Alexander, M. P., & Stuss, D. T. (2009). fMRI evidence of a functional network setting the criteria for withholding a response. *Neuroimage*, 45(2), 537-548. doi:10.1016/j.neuroimage.2008.12.032

Vallesi, A., McIntosh, A. R., Kovacevic, N., Chan, S. C., & Stuss, D. T. (2010). Age effects on the asymmetry of the motor system: evidence from cortical oscillatory activity. *Biol Psychol, 85*(2), 213-218. doi:10.1016/j.biopsycho.2010.07.003

Vallesi, A., & Stuss, D. T. (2010). Excessive sub-threshold motor preparation for non-target stimuli in normal aging. *Neuroimage*, 50(3), 1251-1257. doi:10.1016/j.neuroimage.2010.01.022

van Bochove, M. E., Van der Haegen, L., Notebaert, W., & Verguts, T. (2013). Blinking predicts enhanced cognitive control. *Cogn Affect Behav Neurosci*, 13(2), 346-354. doi:10.3758/s13415-012-0138-2

van Steenbergen, H., & Band, G. P. (2013). Pupil dilation in the Simon task as a marker of conflict processing. *Front Hum Neurosci*, 7, 215. doi:10.3389/fnhum.2013.00215

van Steenbergen, H., Band, G. P., & Hommel, B. (2015). Does conflict help or hurt cognitive control? Initial evidence for an inverted U-shape relationship between perceived task difficulty and conflict adaptation. *Front Psychol*, 6, 974. doi:10.3389/fpsyg.2015.00974

Van de Weghe, P., & Bruggeman, W. (2006). *The impact of the number of performance measures and incentive framing on performance in a multidimensional task environment*. Retrieved from Univ. Gent:

van den Wildenberg, W. P., van Boxtel, G. J., van der Molen, M. W., Bosch, D. A., Speelman, J. D., & Brunia, C. H. (2006). Stimulation of the subthalamic region facilitates the selection and inhibition of motor responses in Parkinson's disease. *J Cogn Neurosci, 18*(4), 626-636. doi:10.1162/jocn.2006.18.4.626

van den Wildenberg, W. P., Wylie, S. A., Forstmann, B. U., Burle, B., Hasbroucq, T., & Ridderinkhof, K. R. (2010). To head or to heed? Beyond the surface of selective action inhibition: a review. *Front Hum Neurosci, 4*, 222. doi:10.3389/fnhum.2010.00222

van Dijk, H., Nieuwenhuis, I. L., & Jensen, O. (2010). Left temporal alpha band activity increases during working memory retention of pitches. *Eur J Neurosci, 31*(9), 1701-1707. doi:10.1111/j.1460-9568.2010.07227.x

van Dijk, H., Schoffelen, J. M., Oostenveld, R., & Jensen, O. (2008). Prestimulus oscillatory activity in the alpha band predicts visual discrimination ability. *J Neurosci, 28*(8), 1816-1823. doi:10.1523/jneurosci.1853-07.2008

van Ede, F., de Lange, F., Jensen, O., & Maris, E. (2011). Orienting attention to an upcoming tactile event involves a spatially and temporally specific modulation of sensorimotor alpha- and beta-band oscillations. *J Neurosci, 31*(6), 2016-2024. doi:10.1523/jneurosci.5630-10.2011

van Elk, M., van Schie, H. T., van den Heuvel, R., & Bekkering, H. (2010). Semantics in the motor system: motor-cortical Beta oscillations reflect semantic knowledge of end-postures for object use. *Front Hum Neurosci, 4*, 8. doi:10.3389/neuro.09.008.2010

Van Iddekinge, C. H., Aguinis, H., Mackey, J. D., & DeOrtentiis, P. S. (2018). A meta-analysis of the interactive, additive, and relative effects of cognitive ability and motivation on performance. *J Managt, 44*(1), 249-279.

van Steenbergen, H., Band, G., & Hommel, B. (2009). Reward counteracts conflict adaptation. Evidence for a role of affect in executive control. *Psychol Sci, 20*(12), 1473-1477. doi:10.1111/j.1467-9280.2009.02470.x

van Steenbergen, H., Band, G., & Hommel, B. (2012). Reward valence modulates conflict-driven attentional adaptation: electrophysiological evidence. *Biol Psychol, 90*(3), 234-241. doi:10.1016/j.biopsycho.2012.03.018

Van Steveninck, A. L., Mandema, J. W., Tuk, B., Van Dijk, J. G., Schoemaker, H. C., Danhof, M., & Cohen, A. F. (1993). A comparison of the concentration-

effect relationships of midazolam for EEG-derived parameters and saccadic peak velocity. *Br J Clin Pharmacol, 36*(2), 109-115. doi:10.1111/j.1365-2125.1993.tb04205.x

van Wijk, B. C., Beek, P. J., & Daffertshofer, A. (2012). Differential modulations of ipsilateral and contralateral beta (de)synchronization during unimanual force production. *Eur J Neurosci, 36*(1), 2088-2097. doi:10.1111/j.1460-9568.2012.08122.x

Van Winsum, W., Sergeant, J., & Geuze, R. (1984). The functional significance of event-related desynchronization of alpha rhythm in attentional and activating tasks. *Electroencephalogr Clin Neurophysiol, 58*(6), 519-524. doi:10.1016/0013-4694(84)90042-7

Vanderveldt, A., Green, L., & Rachlin, H. (2017). Discounting by probabilistic waiting. *J Behav Decis Making, 30*(1), 39-53. doi:10.1002/bdm.1917

Vanni, S., Revonsuo, A., & Hari, R. (1997). Modulation of the parieto-occipital alpha rhythm during object detection. *J Neurosci, 17*(18), 7141-7147. doi:10.1523/jneurosci.17-18-07141.1997

Vasey, M. W., & Thayer, J. F. (1987). The continuing problem of false positives in repeated measures ANOVA in psychophysiology: A multivariate solution. *Psychophysiol, 24*(4), 479-486. doi:10.1111/j.1469-8986.1987.tb00324.x

Vassena, E., Holroyd, C. B., & Alexander, W. H. (2017). Computational models of anterior cingulate cortex: at the crossroads between prediction and effort. *Front Neurosci, 11*, 316. doi:10.3389/fnins.2017.00316

Vaurio, R. G., Simmonds, D. J., & Mostofsky, S. H. (2009). Increased intra-individual reaction time variability in attention-deficit/hyperactivity disorder across response inhibition tasks with different cognitive demands.

Neuropsychologia, 47(12), 2389-2396. doi:10.1016/j.neuropsychologia.2009.01.022

Veldhuizen, R. J., Jonkman, E. J., & Poortvliet, D. C. (1993). Sex differences in age regression parameters of healthy adults--normative data and practical implications. *Electroencephalogr Clin Neurophysiol, 86*(6), 377-384. doi:10.1016/0013-4694(93)90133-g

Verbruggen, F., & Logan, G. D. (2008). Response inhibition in the stop-signal paradigm. *Trends Cognitive Sci, 12*(11), 418-424. doi:10.1016/j.tics.2008.07.005

Verbruggen, F., & McLaren, R. (2018). Effects of reward and punishment on the interaction between going and stopping in a selective stop-change task. *Psychol Res*, 82(2), 353-370. doi:10.1007/s00426-016-0827-5

Verbruggen, F., Stevens, T., & Chambers, C. D. (2014). Proactive and reactive stopping when distracted: an attentional account. *J Exp Psychol Hum Percept Perform, 40*(4), 1295-1300. doi:10.1037/a0036542

Verguts, T., Vassena, E., & Silvetti, M. (2015). Adaptive effort investment in cognitive and physical tasks: a neurocomputational model. *Front Behav Neurosci, 9*, 57. doi:10.3389/fnbeh.2015.00057

Visani, E., Mariotti, C., Nanetti, L., Mongelli, A., Castaldo, A., Panzica, F., . . . Canafoglia, L. (2019). Different patterns of movement-related cortical oscillations in patients with myoclonus and in patients with spinocerebellar ataxia. *Clin Neurophysiol, 130*(5), 714-721. doi:10.1016/j.clinph.2019.01.021

Volkow, N. D., Wang, G. J., Newcorn, J. H., Kollins, S. H., Wigal, T. L., Telang, F., . . . Swanson, J. M. (2011). Motivation deficit in ADHD is associated with

dysfunction of the dopamine reward pathway. *Mol Psychiatry, 16*(11), 1147-1154. doi:10.1038/mp.2010.97

Volkow, N. D., Wise, R. A., & Baler, R. (2017). The dopamine motive system: implications for drug and food addiction. *Nat Rev Neurosci, 18*(12), 741-752. doi:10.1038/nrn.2017.130

Von Neumann, J., & Morgenstern, O. (1947). *Theory of games and economic behavior, 2nd rev*. Princeton, New Jersey, United States: Princeton University Press.

von Stein, A., Chiang, C., & Konig, P. (2000). Top-down processing mediated by interareal synchronization. *Proc Natl Acad Sci, 97*(26), 14748-14753. doi:10.1073/pnas.97.26.14748

Von Stumm, S., Hell, B., & Chamorro-Premuzic, T. (2011). The hungry mind: intellectual curiosity is the third pillar of academic performance. *Perspect Psychol Sci, 6*(6), 574-588. doi:10.1177/1745691611421204

Vrana, S. R., Spence, E. L., & Lang, P. J. (1988). The startle probe response: a new measure of emotion? *J Abnormal Psychol, 97*(4), 487. doi:10.1037/0021-843X.97.4.487

Wagner, J., Wessel, J. R., Ghahremani, A., & Aron, A. R. (2018). Establishing a right frontal beta signature for stopping action in scalp EEG: implications for testing inhibitory control in other task contexts. *J Cogn Neurosci, 30*(1), 107-118. doi:10.1162/jocn_a_01183

Walasek, L., & Stewart, N. (2015). How to make loss aversion disappear and reverse: tests of the decision by sampling origin of loss aversion. *J Exp Psychol Gen, 144*(1), 7-11. doi:10.1037/xge0000039

Walton, M. E., Bannerman, D. M., Alterescu, K., & Rushworth, M. F. (2003). Functional specialization within medial frontal cortex of the anterior cingulate for evaluating effort-related decisions. *J Neurosci, 23*(16), 6475-6479. doi:10.1523/JNEUROSCI.23-16-06475.2003

Walton, M. E., Kennerley, S. W., Bannerman, D. M., Phillips, P. E., & Rushworth, M. F. (2006). Weighing up the benefits of work: behavioral and neural analyses of effort-related decision making. *Neural Netw, 19*(8), 1302-1314. doi:10.1016/j.neunet.2006.03.005

Wang, X., & Johnson, J. G. (2012). A tri-reference point theory of decision making under risk. *J Exp Psychol Gen, 141*(4), 743-756. doi:10.1037/a0027415

Wanquier, A. (1998). *EEG and neuropharmachology, in electroencephalography*. Philadelphia, Pennsylvania, United States: Williams and Wilkins.

Ward, N. S., & Frackowiak, R. S. (2003). Age-related changes in the neural correlates of motor performance. *Brain,* 126(Pt 4), 873-888. doi:10.1093/brain/awg071

Ward, N. S., Swayne, O. B., & Newton, J. M. (2008). Age-dependent changes in the neural correlates of force modulation: an fMRI study. Neurobiol Aging, 29(9), 1434-1446. doi:10.1016/j.neurobiolaging.2007.04.017

Warm, J., S., Dember, W., N., & Hancock, P., A. (1996). *Automation and human performance: Theory and applications:* Vigilance and workload in automated systems.

Wascher, E., Rasch, B., Sänger, J., Hoffmann, S., Schneider, D., Rinkenauer, G., . . . Gutberlet, I. (2014). Frontal theta activity reflects distinct aspects of mental fatigue. Biol Psychol, 96, 57-65. doi:10.1016/j.biopsycho.2013.11.010

Weber, B. J., & Huettel, S. A. (2008). The neural substrates of probabilistic and intertemporal decision making. *Brain Res, 1234*, 104-115. doi:10.1016/j.brainres.2008.07.105

Weisz, N., Hartmann, T., Müller, N., Lorenz, I., & Obleser, J. (2011). Alpha rhythms in audition: cognitive and clinical perspectives. *Front Psychol, 2*, 73. doi:10.3389/fpsyg.2011.00073

Welniarz, Q., Dusart, I., Gallea, C., & Roze, E. (2015). One hand clapping: lateralization of motor control. *Front Neuroanat, 9*, 75. doi:10.3389/fnana.2015.00075

Wendt, M., Kiesel, A., Geringswald, F., Purmann, S., & Fischer, R. (2014). Attentional adjustment to conflict strength: evidence from the effects of manipulating flanker-target SOA on response times and prestimulus pupil size. *Exp Psychol*, 61(1), 55-67. doi:10.1027/1618-3169/a000227

Wessel, J. R., & Aron, A. R. (2013). Unexpected events induce motor slowing via a brain mechanism for action-stopping with global suppressive effects. *J Neurosci, 33*(47), 18481-18491. doi:10.1523/jneurosci.3456-13.2013

Wessel, J. R., & Aron, A. R. (2015). It's not too late: The onset of the frontocentral P 3 indexes successful response inhibition in the stop-signal paradigm. *Psychophysiol, 52*(4), 472-480.

Wessel, J. R., & Aron, A. R. (2017). On the globality of motor suppression: unexpected events and their influence on behavior and cognition. *Neuron, 93*(2), 259-280. doi:10.1016/j.neuron.2016.12.013

Westbrook, A., & Braver, T. S. (2015). Cognitive effort: A neuroeconomic approach. *Cogn Affect Behav Neurosci, 15*(2), 395-415. doi:10.3758/s13415-015-0334-y

Westbrook, A., Kester, D., & Braver, T. S. (2013). What is the subjective cost of cognitive effort? load, trait, and aging effects revealed by economic preference. *PloS one, 8*(7), e68210. doi:10.1371/journal.pone.0068210

Wheaton, L., Fridman, E., Bohlhalter, S., Vorbach, S., & Hallett, M. (2009). Left parietal activation related to planning, executing and suppressing praxis hand movements. *Clin Neurophysiol, 120*(5), 980-986. doi:10.1016/j.clinph.2009.02.161

Whitlock, J. R. (2017). Posterior parietal cortex. *Current Biology, 27*(14), R691-R695.

Whittington, M. A., Traub, R. D., Kopell, N., Ermentrout, B., & Buhl, E. H. (2000). Inhibition-based rhythms: experimental and mathematical observations on network dynamics. *Int J Psychophysiol, 38*(3), 315-336. doi:10.1016/S0167-8760(00)00173-2

Wicklund, R., A., & Gollwitzer, P., M. (2013). *Symbolic self completion*: Routledge. London, United Kingdom.

Wiesman, A. I., Heinrichs-Graham, E., Proskovec, A. L., McDermott, T. J., & Wilson, T. W. (2017). Oscillations during observations: Dynamic oscillatory networks serving visuospatial attention. *Hum Brain Mapp, 38*(10), 5128-5140. doi:10.1002/hbm.23720

Wigfield, A., & Eccles, J. S. (2000). Expectancy-value theory of achievement motivation. *Contemp Educ Psychol*, 25(1), 68-81. doi:10.1006/ceps.1999.1015

Williams, A. L., Kuhn, A., Kupsch, A., Tijssen, M., van Bruggen, G., Speelman, H., . . . Brown, P. (2003). Behavioural cues are associated with modulations of

synchronous oscillations in the human subthalamic nucleus. *Brain, 126*(Pt 9), 1975-1985. doi:10.1093/brain/awg194

Williams, A. L., Ponesse, J. S., Schachar, R. J., Logan, G. D., & Tannock, R. (1999). Development of inhibitory control across the lifespan. *Dev Psychol, 35*(1), 205-213. doi:10.1037/0012-1649.35.1.205

Wilkinson, N., & Klaes, M. (2012). *An Introduction to Behavioral Economics.* Houndsmills, Basingstoke: Palgrave Macmillan.

Wilson, T. D. (2004). Strangers to ourselves: Harvard University Press.

Wilson, T. W., McDermott, T. J., Mills, M. S., Coolidge, N. M., & Heinrichs-Graham, E. (2018). tDCS modulates visual gamma oscillations and basal alpha activity in occipital cortices: evidence from MEG. *Cereb Cortex, 28*(5), 1597-1609. doi:10.1093/cercor/bhx055

Wilson, T. W., Mitchell, S. H., Musser, E. D., Schmitt, C. F., & Nigg, J. T. (2011). Delay discounting of reward in ADHD: application in young children. *J Child Psychol Psychiatry, 52*(3), 256-264. doi:10.1111/j.1469-7610.2010.02347.x

Wilson, T. W., Proskovec, A. L., Heinrichs-Graham, E., O'Neill, J., Robertson, K. R., Fox, H. S., & Swindells, S. (2017). Aberrant neuronal dynamics during working memory operations in the aging HIV-infected brain. *Sci Rep, 7*, 41568. doi:10.1038/srep41568

Wise, R. A. (2004). Dopamine, learning and motivation. *Nat Rev Neurosci, 5*(6), 483-494. doi:10.1038/nrn1406

Wise, S. P., Murray, E. A., & Gerfen, C. R. (1996). The frontal cortex-basal ganglia system in primates. *Crit Rev Neurobiol, 10*(3-4), 317-356.

Wisniewski, M. G., Thompson, E. R., & Iyer, N. (2017). Theta- and alpha-power enhancements in the electroencephalogram as an auditory delayed match-to-sample task becomes impossibly difficult. *Psychophysiol, 54*(12), 1916-1928. doi:10.1111/psyp.12968

Wisniewski, M. G., Thompson, E. R., Iyer, N., Estepp, J. R., Goder-Reiser, M. N., & Sullivan, S. C. (2015). Frontal midline θ power as an index of listening effort. *Neuroreport, 26*(2), 94-99. doi:10.1097/WNR.0000000000000306

Wisniewski, M. G. (2017). Indices of Effortful Listening Can Be Mined from Existing Electroencephalographic Data. Ear Hear, 38(1), e69-e73. doi:10.1097/aud.0000000000000354

Wisniewski, M. G., Thompson, E. R., Iyer, N., Estepp, J. R., Goder-Reiser, M. N., & Sullivan, S. C. (2015). Frontal midline θ power as an index of listening effort. Neuroreport, 26(2), 94-99. doi:10.1097/wnr.0000000000000306

Witham, C. L., Riddle, C. N., Baker, M. R., & Baker, S. N. (2011). Contributions of descending and ascending pathways to corticomuscular coherence in humans. *J Physiol, 589*(Pt 15), 3789-3800. doi:10.1113/jphysiol.2011.211045

Witt, J. K. (2017). A role for control in an action-specific effect on perception. J *Exp Psychol Hum Percept Perform*, 43(10), 1791-1804. doi:10.1037/xhp0000447

Wolters, C., A. (1998). Self-regulated learning and college students' regulation of motivation. *J Educat Psychol*, 90(2), 224. doi:10.1037/0022-0663.90.2.224

Worden, M. S., Foxe, J. J., Wang, N., & Simpson, G. V. (2000). Anticipatory biasing of visuospatial attention indexed by retinotopically specific alpha-band electroencephalography increases over occipital cortex. *J Neurosci, 20*(6), Rc63. doi:10.1523/JNEUROSCI.20-06-j0002.2000

Wright, R., A., & Kirby, L., D. (2001). Effort determination of cardiovascular response: an integrative analysis with applications in social psychology. *Advan in Exp Soc Psychol*, 33, 255-307. doi:2001-01410-005

Wright, R. A. (1996). *Brehm's theory of motivation as a model of effort and cardiovascular response*. New York, New York, United States: The Guilford Press.

Wright, R. A. (2008). Refining the prediction of effort: Brehm's Distinction between potential motivation and motivation intensity. *Soc Personal Psychol Compass*, 2(2), 682-701. doi:10.1111/j.1751-9004.2008.00093.x

Wright, R. A., & Rakow, T. (2017). Don't sweat it: re-examining the somatic marker hypothesis using variants of the balloon analogue risk task. *Decision, 4*(1), 52. doi:10.1037/dec0000055

Wright, R. A., Murray, J. B., Storey, P. L., & Williams, B. J. (1997). Ability analysis of gender relevance and sex differences in cardiovascular response to behavioral challenge. *J Pers Soc Psychol*, 73(2), 405-417. doi:10.1037//0022-3514.73.2.405

Wright, R. A., & Pantaleo, G. (2013). Effort processes in achieving performance outcomes: interrelations among and roles of core constructs. *Behav Brain Sci*, 36(6), 705-706; discussion 707-726. doi:10.1017/s0140525x13001180

Wright, R. A., Shaw, L. L., & Jones, C. R. (1990). Task demand and cardiovascular response magnitude: further evidence of the mediating role of success importance. *J Pers Soc Psychol*, 59(6), 1250-1260. doi:10.1037//0022-3514.59.6.1250

Wright, R. A., Williams, B. J., & Dill, J. C. (1992). Interactive effects of difficulty and instrumentality of avoidant behavior on cardiovascular reactivity. *Psychophysiol*, 29(6), 677-686. doi:10.1111/j.1469-8986.1992.tb02045.x

Wu, S., Hitchman, G., Tan, J., Zhao, Y., Tang, D., Wang, L., & Chen, A. (2015). The neural dynamic mechanisms of asymmetric switch costs in a combined Stroop-task-switching paradigm. *Sci Rep, 5*, 10240. doi:10.1038/srep10240

Wu, T., Zang, Y., Wang, L., Long, X., Hallett, M., Chen, Y., . . . Chan, P. (2007). Aging Influence on Functional Connectivity of The Motor Network in the Resting State. *Neurosci Lett*, 422(3), 164-168. doi:10.1016/j.neulet.2007.06.011

Xie, L., Kang, H. C., Xu, Q., Chen, M. J., Liao, Y., Thiyagarajan, M., . . . Iliff, J. J. (2013). Sleep drives metabolite clearance from the adult brain. *Sci, 342*(6156), 373-377. doi:10.1126/science.1241224

Yamagishi, N., Callan, D. E., Goda, N., Anderson, S. J., Yoshida, Y., & Kawato, M. (2003). Attentional modulation of oscillatory activity in human visual cortex. *Neuroimage, 20*(1), 98-113. doi:10.1016/S1053-8119(03)00341-0

Yamagishi, N., Goda, N., Callan, D. E., Anderson, S. J., & Kawato, M. (2005). Attentional shifts towards an expected visual target alter the level of alpha-band oscillatory activity in the human calcarine cortex. *Brain Res Cogn Brain Res, 25*(3), 799-809. doi:10.1016/j.cogbrainres.2005.09.006

Yamanaka, K., Kimura, T., Miyazaki, M., Kawashima, N., Nozaki, D., Nakazawa, K., . . . Yamamoto, Y. (2002). Human cortical activities during Go/NoGo tasks with opposite motor control paradigms. *Exp Brain Res*, 142(3), 301-307. doi:10.1007/s00221-001-0943-2

Yamanaka, K., & Yamamoto, Y. (2010). Single-trial EEG power and phase dynamics associated with voluntary response inhibition. *J Cogn Neurosci*, 22(4), 714-727. doi:10.1162/jocn.2009.21258

Yechiam, E., & Hochman, G. (2013). Losses as modulators of attention: review and analysis of the unique effects of losses over gains. *Psychol Bull, 139*(2), 497-518. doi:10.1037/a0029383

Yechiam, E., Retzer, M., Telpaz, A., & Hochman, G. (2015). Losses as Ecological Guides: Minor Losses Lead to Maximization and not to Avoidance. *Cognition, 139*, 10-17. doi:10.1016/j.cognition.2015.03.001

Yeung, N., Botvinick, M. M., & Cohen, J. D. (2004). The neural basis of error detection: conflict monitoring and the error-related negativity. *Psychol Rev, 111*(4), 931-959. doi:10.1037/0033-295x.111.4.931

Yoto, A., Murao, S., Motoki, M., Yokoyama, Y., Horie, N., Takeshima, K., . . . Yokogoshi, H. (2012). Oral intake of γ-aminobutyric acid affects mood and activities of central nervous system during stressed condition induced by mental tasks. *Amino Acids, 43*(3), 1331-1337. doi:10.1007/s00726-011-1206-6

Yuan, H., Liu, T., Szarkowski, R., Rios, C., Ashe, J., & He, B. (2010). Negative covariation between task-related responses in alpha/beta-band activity and BOLD in human sensorimotor cortex: an EEG and fMRI study of motor imagery and movements. *Neuroimage, 49*(3), 2596-2606. doi:10.1016/j.neuroimage.2009.10.028

Zaaimi, B., Dean, L. R., & Baker, S. N. (2018). Different contributions of primary motor cortex, reticular formation, and spinal cord to fractionated muscle activation. *J Neurophysiol, 119*(1), 235-250. doi:10.1152/jn.00672.2017

Zakzanis, K. K., Leach, L., & Kaplan, E. (1998). On the nature and pattern of neurocognitive function in major depressive disorder. *Neuropsychiatry Neuropsychol Behav Neurol, 11*(3), 111-119.

Zald, D. H., McHugo, M., Ray, K. L., Glahn, D. C., Eickhoff, S. B., & Laird, A. R. (2014). Meta-analytic connectivity modeling reveals differential functional connectivity of the medial and lateral orbitofrontal cortex. *Cereb Cortex, 24*(1), 232-248. doi:10.1093/cercor/bhs308

Zavala, B., Jang, A., Trotta, M., Lungu, C. I., Brown, P., & Zaghloul, K. A. (2018). Cognitive control involves theta power within trials and beta power across trials in the prefrontal-subthalamic network. *Brain, 141*(12), 3361-3376. doi:10.1093/brain/awy266

Zhang, Y., Li, Q., Wang, Z., Liu, X., & Zheng, Y. (2017). Temporal dynamics of reward anticipation in the human brain. *Biol Psychol*, 128, 89-97. doi:10.1016/j.biopsycho.2017.07.011

Zheng, Y., Li, Q., Zhang, Y., Li, Q., Shen, H., Gao, Q., & Zhou, S. (2017). Reward processing in gain versus loss context: an ERP study. *Psychophysiol*, *54*(7), 1040-1053. doi:10.1111/psyp.12855

Zimmerman, B. J. (2013). Theories of self-regulated learning and academic achievement: An overview and analysis. Self-regulated learning and academic achievement, 10-45.